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ERRATA

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- 46, line 12, for *schaumistandi* read *schaumistande*.
 260, line 16, for *Hoplia smalabanicus* read *Hoplias malabanicus*.
 279, line 9 from bottom, for sprinked read sprinkled.
 406, line 19 from bottom, for *Lotochna* read *Lotochena*.
 473, line 11, for froms read forms.
 484, line 11, for cetain read certain.
 613, line 3, for *Cygetois* read *Cygetoes*.
 636, line 15 from bottom, for *cumatodes* read *cumatodes*.

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(ZOOLOGY.)

The Morphology of the Central Nervous System in the Gastropoda
Pulmonata. By HELENE E. BARGMANN, Ph.D., F.L.S.

(PLATES 1-5, Table to face p. 22, and 4 Text-figures.)

[Read 1st November, 1928.]

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I. INTRODUCTION.

This paper deals with a tendency observed in certain groups of Mollusca for the ganglionic components of the nervous system, originally widely separated by long commissures, to become concentrated and fused together in a single mass. This tendency is seen in the Cephalopoda and the Gastropoda, the groups in which the head-region is most highly differentiated, but in this paper I have confined my attention to the Gastropoda Pulmonata alone. My object has been to ascertain the chief ways in which this concentration is brought about, and to discover if the broad lines of ganglionic concentration are correlated with the modifications of other systems, so that the various criteria of relationships are harmoniously developed, or whether the indications of affinity based on one system are at variance with those derived from another.

In 1893-94, Pelseneer indicated the main lines of evolution of the Pulmonate nervous system, and in the same year Pilsbry* (1894) published his classification of the Helices, in which, however, he did not include considerations of the characters of the nervous system, having "neither the requisite time or space," and thinking that "other organs promised results of more immediate utility." In 1900, Pilsbry adopted the degree of approximation of the cerebral ganglia as the distinguishing features of two subdivisions in his classification of the Stylommatophora. From then onwards, the importance of considering the structure of the nervous system in determining the inter-relationships of the Pulmonate subdivisions has become more fully realised. The work of Watson (1915→) and of Hoffman (1924→) has been particularly valuable. A large mass of anatomical and histological detail was collected by Simroth (1910), but no correlations or comparisons with an existing scheme of classification were made.

* Pilsbry, 'Manual of Conchology,' 2nd series, vol. ix, 1894, p. 287.

So much work of importance has been done since then, *i.e.* since 1910, that it seemed profitable to assemble the scattered evidence and supplement it by investigation of the nervous system of as many genera and species of the Pulmonata as it was possible to obtain. This I was enabled to do by the kindness and courtesy of the Trustees of the British Museum (Natural History Section), who placed the stored Pulmonate material at my disposal, and permitted me to work in the Mollusca Studies of the Museum. I also wish to express my gratitude to Mr. G. C. Robson, of the Mollusca Department, for his help and advice during the time that I have been engaged in working out these results.

II. DESCRIPTION OF THREE TYPES OF MOLLUSCAN NERVOUS SYSTEM.

A ring of nervous tissue encircling the œsophagus forms the ground-plan of the Molluscan central nervous system. From this are given off various connectives and commissures, which may bear ganglia at intervals along their course. These ganglia consist of paired buccal, cerebral, and pedal ganglia in the Gastropoda, together with a chain of ganglia constituting the visceral nervous system. The degree of approximation of these ganglia is subject to much variation, wide separation being taken as indicative of an unspecialized type of nervous system, concentration as showing specialization.

(a) The nervous system of *Patella vulgata* (see text-fig. 1) is a diffuse one. The cerebral ganglia (*cb.*) are joined by a long cerebral commissure to one another. The buccal ganglia (*b.*) lie fairly close to the cerebral ganglia, and are joined to one another by two commissures, a short buccal and a long labial commissure, the former being dorsal, the latter passing ventrally to the buccal mass. The other components of the nervous system lie beneath the alimentary canal, and are joined by long pedal and pleural connectives to the cerebral ganglia. The pedal ganglia are not clearly defined and merge imperceptibly into long pedal cords (*pd.*). The pleural ganglia (*pl.*) are large and give off several pallial nerves; they are first in the series of ganglia on the visceral chain. In consequence of the torsion of the visceral mass in the Gastropoda, the visceral chain is twisted into a figure of eight, *i.e.*, it is said to be "chiastoneurous." Besides the pleural ganglia, the visceral chain bears three other ganglia: the supra-intestinal ganglion (*Sup.I.*) on the left, the sub-intestinal ganglion (*Sub.I.*) on the right, and the abdominal ganglion (*Abd.*) between the two. All the ganglia are separated by moderate lengths of visceral commissure. This type of nervous system is characteristic of the subclass Streptoneura, to which *Patella* belongs.

(b) In the second subclass, the Euthyneura, the chiasmoneurous condition of the visceral chain has been lost, except in a few archaic forms, such as the Pulmonate, *Chilina dombeiana* (text-fig. 2) (Plate, 1895). Here, in addition, the pedal centres have become concentrated in two ganglia, and the cerebral commissure and connectives are considerably shorter. The visceral chain, however, is long and twisted, and besides the five ganglia described above, two other ganglia are found on it, the parietal ganglion and

TEXT-FIGS. 1-3.

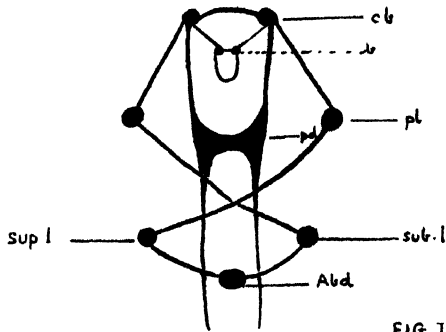


FIG. 1

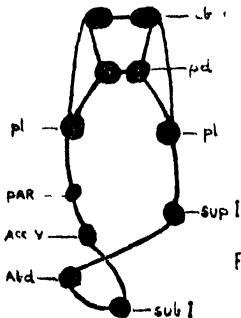


FIG. II

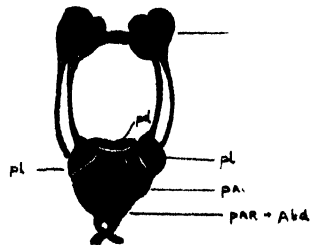


FIG. III

the accessory visceral ganglia, which lie between the left pleural and the subintestinal ganglia. Pelseneer (1893) described the parietal ganglion as a new structure, characteristic of the Pulmonata, and regarded the accessory visceral ganglion as a ganglionic swelling such as is often met with in nervous systems of an unspecialized type.

(c) Such diffuseness in the visceral nervous system is not characteristic of the majority of the Pulmonata, in which, as a rule, a concentrated visceral

chain is found. In *Helix pomatia* (text-fig. 3) the length of the cerebral commissure and connectives is about the same as in *Chilina*, but the cerebral ganglia are definitely lobed, and the visceral ganglia are closely aggregated together, their number being reduced to four, all trace of commissures having disappeared. Obviously here direct fusion has taken place between the components of the visceral chain. The visceral nerves arising from the abdominal ganglion exhibit traces of chiastoneury, as they can be observed to cross over one another just beyond their point of origin.

III. SKETCH OF THE GENERAL EVOLUTION OF THE GASTROPOD NERVOUS SYSTEM UP TO THE PULMONATA.

The general lines along which the evolution of the Gastropod nervous system is assumed to have proceeded all lead to one result, that of concentration of the ganglionic centres in the head-region around the oesophagus. In the Streptoneura the type of nervous system met with in *Patella* is the least specialized. Condensation does take place in some forms, e. g., *Lamellaria* (Pelseneer, 1906), the cerebral and pleural ganglia becoming so closely applied to one another that all trace of the cerebro-pleural connective is lost. The visceral chain also shortens considerably, although it still exhibits the condition of chiastoneury.

In the Opisthobranchia, the chiastoneurous condition is lost in the more specialized forms. In *Acteon* (Pelseneer, 1893), the cerebral and pleural ganglia are very nearly fused together. The visceral chain is still twisted, and consists of five ganglia very widely separated (as in *Patella*). In *Acera* (Pelseneer, 1893) the cerebral and pleural ganglia are not fused, but the visceral chain is untwisted. Pelseneer (1893) claimed fusion of the cerebral and pleural ganglia in *Pleurobranchura*. This was denied by Distaso (1904), who found that the pleural and pedal ganglia were united, and that all the ganglia of the visceral chain, except the abdominal ganglion, have disappeared. It is more usual to have the cerebral and pleural ganglia fused together, with the pedal ganglia closely applied to them, and one ganglion, the abdominal, in the visceral chain, which remains long and slender, e. g., *Tritonia* (Pelseneer, 1893). When further condensation takes place, the visceral chain shortens, bringing the abdominal ganglion nearer to the cerebro-pleural mass on the right side, as in *Goniodoris* (Pelseneer, 1893). As a final stage in the concentration of the nervous system, the abdominal ganglion disappears, leaving only a short visceral commissure between the cerebro-pleural ganglia, e. g., *Eolis* (Pelseneer, 1893).

All stages in the concentration of the nervous system are met with in the

Pulmonata, from forms such as *Chilina dombeiana*, with a long chiasoneurous visceral chain, with seven ganglia on it, to forms showing complete reduction of all commissures and connectives, with consequent approximation and fusion of the ganglionic centres. The first point in the nervous system at which condensation takes place is, again, the visceral chain, which becomes reduced by shortening of the commissure and fusion of the ganglia one with another. But unlike the condition in the Opisthobranchia, the ganglia of the visceral chain fuse "among themselves" primarily, and not with the ganglia of another part of the nervous system, *i.e.*, with the cerebrals or pedals.

I have found it possible to differentiate between eight types of arrangement of the visceral ganglia in the Pulmonata. These types form a very general scheme, based entirely on morphological details of the nervous system alone, and in a later section of this paper the position of the Pulmonate genera and species in this scheme is compared with their position in the accepted scheme of systematic classification based on considerations of other organs, and put forward by Pilsbry (1894).

Before describing the characteristics of these eight types of nervous system, there are some general points of Pulmonate nervous anatomy and histology which must be considered, in order that the identity and fate of various parts of the nervous system may be clearly understood.

IV. PRELIMINARY DESCRIPTION OF THE NERVOUS SYSTEM IN THE PULMONATA.

In 1915, Watson demonstrated the existence of five rings of nervous tissue around the œsophagus in the Pulmonate *Apera*. He said*: "The central nervous system of *Apera* may be regarded as formed of five sections, each with a single pair of ganglia"; and, further, "just as there are five pairs of ganglia, so also are there five commissures ventral to the alimentary canal." These five components are as follows:—(1) The cerebral ganglia with the cerebral and sub-cerebral commissures, to which are united (2) the buccal ganglia, commissure, and connectives. (3) The pedal ganglia, pedal and para-pedal commissures, and pedal connectives. (4) Pleural ganglia, pleural commissure (fibres of which run in the pedal commissure in the Pulmonata, but which is separate in the Neritidæ and Helicinidæ), and pleural connectives. (5) Visceral ganglia, commissure, and connectives. Watson pointed out that few authors have found more than *four* commissures in the

* Watson, "Studies on the Carnivorous Slugs of South Africa," Ann. Natal Gov. Mus., vol. iii, part 2. 1915, p. 152.

Pulmonata ; but there is no apparent reason why *Apera* should be regarded as an exceptional case, and it is probable that further research will show that "normally there are five commissures ventral to the alimentary canal in the Euthyneura."

All the details of the structure of these five components of the Pulmonate nervous system need not be included here, but there are some features which, through their modifications, have bearing on the possible affinities of the members of this class, and therefore must be described.

(a) *Cerebral Ganglia.*

In considering all the types of concentration found amongst the Pulmonata, there is never any doubt as to the identity of the cerebral complex. Although the cerebral ganglia may be approximated to the pedals or to the pleurals, or to both, the cerebral ganglia are always distinct, and, in spite of differences in detail, the nerves, which arise from them, are constant in their distribution.

The shape of the cerebral ganglia varies from a smooth oval form, e.g., *Vallonia costata* (Pl. 1. fig. 13), with a distinct commissure, to a very definite lobed contour, e.g., *Helix pomatia* (Pl. 2. fig. 25), three regions being distinctly noticeable in each ganglion. These have been distinguished as pro-, meso-, and meta-cerebrum by Meisenheimer (1912), and their development seems to indicate a degree of greater specialization than is met with in forms with unlobed cerebral ganglia. This is supported, according to Nabias (1894), by the fact that in some of the more primitive Pulmonata, the Basommatophora, unlobed forms occur.

The exact shape of the cerebral ganglia is often difficult to determine without microscopic investigation, as they may be so closely bound together by connective tissue that it is impossible to dissect them free from it. This is the case in *Apera gibbonsi* (Watson, 1915), and it is only in the smaller species, such as *A. parva* and *A. purcelli*, that the separate oval ganglia can be seen. This variation in the shape of the cerebral ganglia within a genus frequently occurs. [Cf. *Brachypodella agnesiana* (Pl. 3. fig. 42) and *B. bruccidi* (Pl. 3. fig. 43).]

The degree of approximation of the cerebral ganglia one with the other also varies. The commissure may be long (*Chilina mulleri*, Pl. 1. fig. 2) ; moderate (*Vallonia costata*, Pl. 1. fig. 13) ; reduced, so that the ganglia touch one another (*Ashmunella cockerelli*, Pl. 2. fig. 21) ; or, finally, the ganglia may be fused (*Oxytyle bensoni*, Pl. 3. fig. 38).

(b) *Buccal Ganglia.*

The buccal ganglia, also, though they may approximate to one another, never tend to fuse with the cerebral ganglia, and their identity is always

Chilina dombeyana is the only recorded instance of a chiastoneurous visceral chain occurring in the Pulmonata. Pelseneer (1906) regarded the straightening of the visceral chain as being brought about by secondary detorsion of the visceral mass during development. Naef (1911) maintained that the concentration of the nervous system in the head-region in the Pulmonata had led to a gradual shortening of the visceral chain, and to its apparent untwisting. He supported his theory by a series of diagrams of the visceral mass and pallial organs in a chiastoneurous Prosobranch and a so-called "detorted" Pulmonate (Pl. 5. fig. 66). These figures show that the position of the pallial organs is the same in the Prosobranchia as in the Pulmonata, whereas in the Opisthobranchia (Pl. 5. fig. 67) detorsion is accompanied by definite shifting of the pallial organs. The work of Merker (1913) (Pl. 5. fig. 65) lends additional evidence to Naef's contention, and he points out that in some of the more specialized Pulmonates, crossing of the visceral nerves from right to left, and *vice versâ*, can still be distinctly seen, e. g., *Helix pomatia*.

Pelseneer (1893), working on *Chilina mulleri* (Pl. 1. fig. 2), found an untwisted visceral chain; it is interesting to note the degree of variation existing within this genus. The left pleural and sub-intestinal ganglia are closely approximated. The abdominal ganglion is widely separated from them, and from the bilobed supra-intestinal ganglion, which in its turn has a moderate length of commissure separating it from the right pleural ganglion. In Pelseneer's figure of the nervous system of *Chilina mulleri* (Pl. 1. fig. 2) a slight swelling, from which a nerve arises, is shown on the visceral chain between the sub-intestinal and abdominal ganglion (marked X in Pl. 1. fig. 2). No mention of this ganglion or its nerve is made in the text, but it seems very likely that the visceral ganglia should be more correctly named as follows:—

- | | |
|---|--|
| 1. Left pleural ganglion | No nerves. |
| 2. Left parietal ganglion | Not sub-intestinal, as it gives off a pallial nerve. |
| 3. Sub-intestinal ganglion | Marked X in figure. |
| " " " | 1 nerve (destination unknown). |
| 4. Abdominal ganglion | 1 visceral nerve. |
| 5. Supra-intestinal ganglion | 1 osphradial nerve. |
| " " " | 1 pallial nerve. |
| 6. Right pleural ganglion | No nerves. |

This suggested renaming is further justified by Pelseneer's (1900) account of *Latia neritoides* (Pl. 1. fig. 3) and comparison with *Chilina*. In *Latia* the pleural ganglia give rise to a long, untwisted visceral chain, the right side of which is higher than the left, a remnant of the chiastoneurous condition. The left parietal ganglion lies close to the left pleural ganglion,

and is widely separated from the sub-intestinal ganglion, which lies close to the abdominal ganglion, though it is quite distinct from it. The abdominal ganglion is joined to the supra-intestinal ganglion by a long stretch of commissure, the supra-intestinal ganglion being bilobed, innervating the osphradium and mantle, and lying close to the right pleural ganglion. Pelsenæer, in this paper, compares the left parietal ganglion of *Latia* with that of *Chilina*, and, although there was no mention of a parietal ganglion in his original description of the visceral chain of the latter, he does not suggest any correction to his previous figure of this type.

According to most workers, five ganglia are usually found on the visceral chain in the Pulmonata, united together in varying degrees of concentration. The condition met with in *Marinula juanensis* (Pl. 1. fig. 7) is very typical of an unspecialised type of nervous system. The description is given by Odhner (1925). The five visceral ganglia are separated from one another by short lengths of commissure. They consist of :—

- | | |
|----------------------------------|-------------------|
| 1. Left pleural ganglion | No nerves. |
| 2. Left parietal ganglion | 1 nerve figured. |
| 3. Abdominal ganglion | 1 nerve figured. |
| 4. Right parietal ganglion | 2 nerves figured. |
| 5. Right pleural ganglion | No nerves. |

An asymmetrical appearance is due to the fact that the abdominal ganglion lies rather nearer to the right parietal than the left, and that of the left cerebro-pleural connective is twice as long as the right. The areas of innervation of the visceral nerves are unfortunately not described.

The same nomenclature for these five ganglia is not used by all authors. Simroth (1910) suggests the adoption of the following names, homologizing the visceral ganglia of the Pulmonata with those of the Prosobranchia :—

<i>Pulmonata.</i>	<i>Prosobranchia.</i>
1. Left pleural ganglion.	Left pleural ganglion.
2. Left parietal ganglion.	Missing.
3. Abdominal segment.	Sub-intestinal and abdominal ganglion.
4. Right parietal ganglion.	Supra-intestinal ganglion.
5. Right pleural ganglion.	Right pleural ganglion.

Simroth's scheme will be adhered to from now onwards in this paper, and, for the sake of clearness, his nomenclature will be given, in addition, in all cases where authors have adopted an alternative one.

The question of the number and distribution of the visceral nerves is a very important one in determining the identities of the ganglia. In the

primitive form *Chilina dombeiana* the nerve-supply from the visceral ganglia was noted by Plate (1895). The following table shows it in comparison with the nerve-supply from the five visceral ganglia in *Helix pomatia*, which was worked out by Schmalz (1914) and confirmed by the histological investigations of Kunze (1919) :—

CHILINA DOMBEIANA. HELIX POMATIA.

Ganglia.	Nerves.	
1. Left pleural.	No nerves.	2—nervus musculi columellaris. nervus musculi retractoris pharyngealis 1—nervus pallialis sinister.
2. Left parietal.	1 pallial.	
3. Acc. visceral (only in <i>Chilina</i>).	1 nerve (destination unknown).	
4. Sub-intestinal (only in <i>Chilina</i>).	1 nerve (mantle and rectum).	
5. Abdominal.	1 nerve (intestine.) 1 nerve (pericardium, kidney, and geni- talia).	3—nervus cutaneus pallialis. nervus analis. nervus intestinalis (pericardium, kidney, genitalia).
6. Supra-intestinal.	1 nerve (osphradial). 1 nerve (pallial).	3—nervus pallialis externus. nervus pallialis internus. nervus aortæ.
7. Right pleural.	No nerves.	2 nerves as above from left pleural.

When the primitive number of seven visceral ganglia is reduced to five by condensation, fusion takes place between the sub-intestinal and abdominal ganglia (presumably the accessory visceral ganglion, only described in the case of *Chilina dombeiana*, is also absorbed). This is shown by the nerve-supply in *Helix* from the composite abdominal ganglion. The supra-intestinal ganglion is regarded by most workers as being homologous with the right parietal ganglion; whereas the left parietal ganglion is a new structure, characteristic of the Pulmonata alone. However, the fact that bilobed supra-intestinal ganglia have been figured and described in primitive Pulmonates (e. g., *Chilina* and *Latia*) rather suggests that the right parietal ganglion also arose as a separate structure, which becomes fused with the supra-intestinal ganglion when condensation takes place.

It will be seen by the table above that the pleural ganglia in *Chilina* do not give rise to nerves. At one time this was believed by many authors to be the invariable rule. Amaudrut (1898) was the first to show that this was erroneous, and since then other workers have reported the occurrence of nerves arising from the pleural ganglia. Schmalz (1914) and Kunze (1919) were the first to give a detailed account of the origin and distribution of the visceral nerves—the former anatomically, the latter histologically. The two

workers confirm one another's results, and Schmalz's account of the distribution of the nerves is given here :—

TWO PLEURAL GANGLIA.

1. *Nervus musculi columellaris* to the retractor muscle of the columella in which it branches.
2. *Nervus musculi retractoris pharyngealis*. to retractor muscle of the buccal mass, by way of the œsophageal nerve-ring. One branch anastomoses with the buccal nerve.

LEFT PARIETAL.

3. *Nervus pallialis sinister* to mantle-edge and roof on the left side.

RIGHT PARIETAL.

4. *Nervus pallialis dexter internus* . . . Internal pallial nerve to region of respiratory aperture and outer right edge of mantle.
5. *Nervus pallialis dexter externus* External pallial nerve to inner right mantle-edge.
6. *Nervus aortæ* to aorta.

ABDOMINAL.

7. *Nervus cutaneus pallialis* to body-wall below the mantle and to the mantle itself.
8. *Nervus analis* to rectum, ureter, mantle-edge, and anal region.
9. *Nervus intestinalis* to aorta, kidney, liver, pericardium, albumen gland, hermaphrodite gland and duct, intestine and body-wall over the visceral mass.

It is in the course of the nerves from the abdominal ganglion that remnants of chiasmoneury can still sometimes be traced. These nerves cross over one another in their course soon after their point of origin (Pl. 2. fig. 25).

Eleven visceral nerves have not been recorded by many workers, as the pleural ganglia are not generally considered to give rise to nerves, and some of the smaller nerves are difficult to demonstrate, except in large specimens or by the employment of histological methods. I was able to find one pair of pleural nerves to the retractor pharyngeal muscles in *Placostylus bivaricosus* (Pl. 2. fig. 25), but in the larger forms, which I have dissected, nerves which appear to be pleural in origin can be shown to originate in the pedal ganglia when freed from the connective-tissue covering.

Another complication also arises in determining the origin of these nerves, that of the close approximation and partial fusion of the pleural and pedal centres. In a fairly diffuse nervous system the pleural ganglia are joined to the pedal ganglia by short but distinct pleuro-pedal connectives,

through which, according to Watson (1915), run fibres from one pleural centre across the pedal commissure to the other pleural centre (see p. 6). As condensation proceeds, the connective shortens and finally, in concentrated forms, disappears altogether, the pleural and pedal ganglia being often partially united. In such cases, careful observation is necessary to distinguish between pleural and pedal nerves, since the limits of the ganglia are difficult to define, and, even in instances where a very short pleuro-pedal connective is apparent, nerves sometimes arise indiscriminately from the two ganglia and from the connective between them. It is therefore important to ascertain the distribution of the pedal nerves so that some distinction can be made.

The pedal nerves are numerous and their roots are generally bound together by connective tissue, which makes their number difficult to determine. Schmalz (1814) and Kunze (1919), working on *Helix pomatia*, found ten pairs of nerves to the pedal muscles—*nervi musculi pedales*—and three pairs of nerves to the body-wall (including the genital apparatus on the right side)—*nervi cutanei pedales*. These last three pairs have been reported by other workers, and correspond to the "nerves of the neck" of Lacaze-Duthiers (1872 A). The *nervi musculi pedales* arise ventrally, and laterally and posteriorly; the *nervi cutanei pedales* arise dorsally and anteriorly in the neighbourhood of the pleuro-pedal connective.

In *Apera*, Watson (1915) reports that one pair of nerves arises from the pleural ganglia, one from the pleuro-pedal connective, and one from the pedal ganglia, and he regards them as corresponding to the "nerves of the neck" of Lacaze-Duthiers, since they innervate the body-wall. He states * that this lends support to the theory that "the outer dorsal portions of the pedal ganglia of most Gastropods are in reality parts of the pleural nerve centres, which have become united with the pedal ganglia, and that all the 'nerves of the neck' therefore spring from the pleural division of the central nervous system." It is evident that the reverse fusion has taken place, and that the pedal ganglia in *Apera* have become united with the pleural ganglia, and the apparent "pleural" nerves are really the three *nervi cutanei pedales*, since their distribution is not that of *true* pleural nerves.









Mention has been made of the connective-tissue sheath (wrapping over the pedal ganglia) and nerves. This sheath is found in many forms enveloping the whole central nervous system; it successfully masks the contours of the ganglia, and in very condensed types makes the number and mode of fusion of the ganglia very difficult to determine without histological investigation.

* Watson, "Carnivorous Slugs of South Africa," Ann. Natal Gov. Mus., vol. iii, part 2, 1915, p. 150.

V. DESCRIPTION OF THE EIGHT TYPES OF PULMONATE NERVOUS SYSTEM.

The eight types into which the nervous system of the Pulmonata can be broadly classed are as follows:—

TEXT-FIG. 4.

- | | | |
|---|-----------------------------------|--|
|  | 1. Basommatophoran type | Five visceral ganglia, slightly separated by lengths of commissure. |
|  | 2. Zonitoid type | Five visceral ganglia, all in contact, but distinguishable from one another. |
|  | 3. Orthurethran type . . | Four visceral ganglia, reduction in number being due to fusion of the right parietal with the abdominal ganglion. |
|  | 4. Heliciform type | Four visceral ganglia, reduction in number being due to fusion of the left parietal with the abdominal ganglion. |
|  | 5. <i>Hygromia</i> type . . . | Three visceral ganglia, reduction in number being due to fusion of the left parietal with abdominal ganglion, and of the right parietal with the right pleural ganglion. |
|  | 6. <i>Ennea</i> type | Three visceral ganglia, reduction in number being due to fusion of the two parietal ganglia with the abdominal ganglion. |
|  | 7. <i>Onchidium</i> type . . | Three visceral ganglia, reduction in number being due to fusion of the parietal with the pleural ganglia. |
|  | 8. <i>Vaginula</i> type | All the visceral ganglia form a fused mass. |

(The buccal ganglia are not shown in these eight diagrams.)

The three most primitive forms of nervous system, *Chilina dombeiana*, *Chilina mulleri*, and *Latia neritoides* (described on pp. 8, 9, and 10), are

not included in this scheme, which is based on the different ways in which concentration of the visceral ganglia can take place. Perfectly clearly-defined examples of each type have, in my opinion, justified the adoption of this scheme, though some of the types, as such, are more readily recognizable than others. For instance, Type I is always a distinct one, from the fact that the visceral ganglia are separated by lengths of commissure. Types II, III, and IV are sometimes difficult to distinguish if the ganglia are closely fused or much covered with connective tissue, and can be confused with Type VIII. Generally speaking, I have found that the types are clearly defined, however, and I have indicated the dubious examples when they occur. Descriptions of typical examples of each type are now given:—

1. *Basommatophoran type*, e.g., *Marinula juanensis* (Pl. 1. fig. 7). (Odhner, 1925.)—This has already been referred to (p. 10) as being a typical example of an unspecialized form of nervous system. The cerebral ganglia are oval in shape and the commissure is of moderate length. An appearance of asymmetry is given to the visceral chain by the fact that the left cerebro-pleural connective is twice as long as the right. The visceral ganglia are all separated from one another by lengths of visceral commissure. The abdominal ganglion lies much nearer to the right parietal ganglion than to the left. Visceral nerves are figured arising from the parietal and abdominal ganglia, but no description of their distribution is given. The pleuro-pedal connectives are well marked, and Odhner figures one long pedal commissure.

2. *Zonitoid type*, e.g., *Zonites cellarius* (Pl. 4. fig. 56).—Lacaze-Duthiers (1872, p. 151) figures the nervous system of *Zonites* in his paper on the Otocysts of Molluscs, but does not give a very detailed description. He says: "Le système nerveux central est moins concentré, ses éléments sont un peu plus éloignés les uns les autres, et le collier œsophagien est relativement beaucoup plus allongé. Le groupe inférieur, composé de cinq amas de cellules fort distinctes, ne repose plus, comme dans les *Helix* et les *Limax*, sur la face postérieure des ganglions pédieux, il est plus bas." He figures visceral nerves arising from the parietal and abdominal ganglia, but does not describe their distribution.

3. *Orthurethran type*, e.g., *Vallonia costata* (Pl. 1. fig. 13). (Watson, 1920.)—The cerebral commissure is narrow and fairly long, being about equal in length to the greatest breadth of the ganglia, which are elongated lengthways. The cerebro-pleural connectives are considerably shorter than the cerebro-pedal connectives. The pleural ganglia are distinct in the visceral chain. The left parietal is separated from the left pleural ganglion and from the abdominal ganglion by short lengths of commissure. The right parietal ganglion is almost fused with the abdominal ganglion and

closely approximated to the right pleural ganglion. The visceral chain lies anterior to the pedal ganglia. The visceral nerves are not described.

4. *Heliciform type*, e. g., *Helix pomatia* (Pl. 2. fig. 25). (*Schmalz*, 1914.)—The cerebral ganglia are trilobed, and are joined by two distinct commissures, cerebral and sub-cerebral. The cerebro-pleural and cerebro-pedal connectives are of equal length, and the visceral ganglia lie on top of the pedal ganglia. There are two pedal commissures. The visceral ganglia are very concentrated, being closely bound together by connective tissue; no visceral commissure is apparent. The pleural ganglia are distinct, but the left parietal is almost completely fused with the abdominal ganglion. The right parietal ganglion remains distinct. There are eleven visceral nerves. (See p. 12.)

5. *Hygromia type*, e. g., *Hygromia limbata* (Pl. 3. fig. 31). (*Watson*, 1918, p. 124.)—The cerebral ganglia are distinctly lobed, and the cerebral commissure is "about equal in length to the breadth of each ganglion." The cerebro-pleural and the cerebro-pedal connectives are very long. The pedal ganglia approximate in the middle line. "The visceral ganglia show a considerable amount of concentration, for not only is the left parietal ganglion fused with the abdominal, but the right parietal ganglion is practically united with the right pleural ganglion." Watson does not describe or figure the distribution of the nerves.

6. *Ennea type*, e. g., *Ennea dussmieri* (Pl. 4. fig. 53).—*Wiegmann* and *v. Martens* (1898) described the nervous system of *Ennea*. The cerebral ganglia are slightly lobed and joined by a very short commissure. The cerebro-pleural and cerebro-pedal connectives are of equal length and fairly long. The pedal ganglia approximate in the middle line, and the pleural ganglia are united to them by very short connectives. There is a considerable length of visceral commissure between the pleural ganglia and the fused mass, formed by the union of the parietal and abdominal ganglia. Six visceral nerves arise from this mass. I give *Wiegmann's* description of their destination and compare them with those of *Helix pomatia* described by *Schmalz* (p. 12):—

WIEGMANN.	SCHMALZ.
I. Left pallial nerve.	Nervus pallialis sinister.
II. To body-wall.	„ cutaneus pallialis.
III. Genital nerve.	„ intestinalis.
IV. To right mantle-edge.	„ analis.
V. Right pallial nerve.	„ pallialis dexter l.
VI. Unknown distribution.	„ „ „ II.

7. *Onchidium type*, e. g., *Onchidella capensis* (Pl. 5. fig. 61). (*Watson*, 1925, pp. 255-58.)—The lateral lobes of the cerebral ganglia are well

developed. There are two commissures—the cerebral, thick and arched, and the sub-cerebral, more slender, but “better developed than in most Stylomatophora.” The pedal ganglia are united to the cerebral ganglia by an “unusually large connective.” They are joined together by two commissures. The visceral ganglia comprise “the right and left pleuro-parietal ganglia, and the median abdominal ganglion. The former are joined to the corresponding pedal ganglia by quite short pleuro-pedal connectives, and to the cerebral ganglia by almost equally short cerebro-pleural connectives.” The abdominal ganglion is joined to the pleuro-parietal ganglia by unequal lengths of visceral commissure, the right being twice as long as the left. Three large pallial nerves arise from the pleuro-parietal ganglia and innervate the mantle, but two are often joined at their origin, and probably correspond to the internal and external pallial nerves of *Helix*. The abdominal ganglion gives off two large nerves, corresponding to the anal and intestinal nerves of *Helix*.

8. *Vaginula type, e. g., Meisenheimeria alte.* (Hoffmann, 1926.)—It is difficult to distinguish the number of visceral ganglia in this example, even histologically. The exit of the nerves gives the only clue, though externally a number of indentations show on the posterior surface of the fused mass. Hoffmann records the occurrence of six visceral nerves, and describes their origin and the homologies of the various divisions of the visceral complex.

The central division gives rise to three (or four) visceral nerves:—

- (1) *Nervus intestinalis*, on the right to heart and viscera.
- (2) *Nervus pallialis quartus dexter*, which divides into two main branches:
 - (a) *Nervus genitalis*, to reproductive system.
 - (b) *Nervus intestinalis*, to rectum and ureter.
- (3) *Nervus pallialis quartus sinister*, which is often divided into two at its origin, giving the appearance of four nerves.

This division is evidently the *abdominal ganglion*. To the right are two more divisions, which correspond to the *right parietal* and *right pleural ganglia*. Nerves originate from both divisions, and, as Hoffmann believes that a *true* pleural ganglion never gives off nerves, he maintains that fusion has taken place with the parietal ganglion. The nerves are: (1) *Nervus cutaneus*, to head-region; (2) *Nervus pallialis, primus*, and *secundus* and *tertius*, the last two having a common origin.

On the left side the parietal ganglion is subdivided into two, one part of which may be a primitive accessory ganglion such as is met with in *Chilina*. The three pallial nerves originate separately on the left side.

VI. VARIATION WITHIN SPECIES.

The question of variation with age of the position of the ganglia in the Pulmonate nervous system is one which must be considered, for it is possible that a certain amount of concentration and shortening of connectives and commissures may take place as the animal matures. If this is the case, it is also possible that workers might have described the nervous system of a young animal which appeared to belong to one type, whereas, had the specimen been mature, concentration of the ganglia might have taken place, which would have altered the type of nervous system. For example, Type I might pass into Type II with condensation, or Type II into Type III, and so on.

With this in view, I have examined 25 examples of Type I, 25 of Type II, and 64 of Type IV, some of the specimens being mature, some immature. The following measurements of the nervous system were taken :—

1. Breadth of cerebral ganglia, between exits of the pedal connectives.
2. Length of cerebro-pleural connectives, left and right.
3. Length of cerebro-pedal connectives, left and right.
4. Length of visceral chain.

The second and third measurements are more subject to personal error than the other two, since, previous to their determination, a certain amount of dissection is necessary in some specimens, which may stretch the connectives. It is also difficult to straighten them out sufficiently for accurate measurement without due stretching. I have endeavoured to check my observations by re-measurement after an interval of time. *Limnaea stagnalis* was selected as an example of Type I, *Macrochlamys versica* for Type II, and *Helix aspersa* (50) and *Placostylus binaricosus* (14) for Type IV.

*Measurements of the Nervous System, expressed as percentages
of the length of shell.*

Helix aspersa.

Immature Forms.

Length of shell.	Breadth of cerebral ganglion. Per cent.	Cerebro-pleural connectives.		Cerebro-pedal connectives.		Length of visceral chain. Per cent.
		Left. Per cent.	Right. Per cent.	Left. Per cent.	Right. Per cent.	
1. 1.00 cm.	30.00	40.00	40.00	30.00	35.00	11.00
2. 1.05 „	26.65	33.38	28.60	33.38	28.60	11.43
3. 1.15 „	24.18	30.43	26.04	26.04	26.04	8.70
4. 1.15 „	26.10	34.80	30.25	34.80	30.26	10.45
5. 1.20 „	20.83	33.18	25.00	25.00	25.00	10.00

Helix aspersa (cont.).

Immature Forms.

Length of shell.	Breadth of cerebral ganglion. Per cent.	Cerebro-pleural connectives.		Cerebro-pedal connectives.		Length of visceral chain. Per cent
		Left. Per cent	Right. Per cent.	Left. Per cent.	Right. Per cent.	
6. 1.25 cm.	24.00	32.00	32.00	28.00	28.00	9.60
7. 1.30 „	17.70	30.79	30.79	23.05	23.06	9.27
8. 1.50 „	19.35	26.35	23.36	20.00	20.00	8.00
9. 1.50 „	19.35	26.70	20.00	23.36	23.36	9.35
10. 1.50 „	20.00	23.36	20.00	20.00	20.00	9.35
11. 1.50 „	15.35	23.36	20.00	16.68	16.68	7.34
12. 1.60 „	18.75	18.75	18.75	18.75	15.16	8.75
13. 1.65 „	18.18	24.12	20.11	15.16	12.13	6.13
14. 1.65 „	19.40	24.12	18.18	18.18	15.16	7.26
15. 1.65 „	18.18	27.15	24.12	24.12	18.18	7.85
16. 2.00 „	16.00	22.50	20.00	15.00	15.00	7.50
17. 2.00 „	17.00	27.50	25.00	25.00	25.00	7.00
18. 2.16 „	13.00	23.25	18.59	18.59	16.27	3.72
19. 2.20 „	15.92	27.25	22.68	25.00	22.68	5.00
20. 2.35 „	13.60	19.15	19.15	17.05	17.05	5.12
21. 2.35 „	14.70	22.23	22.23	17.80	22.23	4.45
22. 2.35 „	16.60	27.68	24.47	25.54	24.47	4.68
23. 2.40 „	12.80	20.85	20.85	18.75	16.69	4.15

Mature Forms.

24. 2.35 cm.	14.80	25.54	24.47	27.68	25.54	4.45
25. 2.45 „	14.30	24.50	20.42	20.42	20.42	6.15
26. 2.50 „	12.00	24.00	20.00	22.00	20.00	5.60
27. 2.50 „	14.00	24.00	20.00	20.00	16.00	5.20
28. 2.55 „	12.20	21.58	19.62	17.67	17.67	3.92
29. 2.55 „	11.40	19.62	19.62	17.67	15.71	3.92
30. 2.55 „	11.80	19.62	15.71	15.17	13.75	3.92
31. 2.55 „	13.70	23.52	21.58	21.58	21.58	4.70
32. 2.60 „	11.90	23.07	19.25	19.25	19.25	5.00
33. 2.60 „	12.30	28.89	26.92	23.07	23.07	4.23
34. 2.60 „	13.50	26.92	25.00	23.09	19.25	4.23
35. 2.60 „	15.00	26.92	23.07	25.00	23.07	4.23
36. 2.65 „	11.33	20.80	18.80	17.00	14.55	5.87
37. 2.65 „	13.60	22.68	20.08	22.68	20.08	3.78
38. 2.70 „	11.86	18.54	17.32	13.47	15.40	6.54
39. 2.75 „	10.80	18.86	14.55	16.38	14.55	5.45
40. 2.75 „	11.60	25.45	21.82	18.19	16.39	4.00
41. 2.75 „	12.80	20.00	18.18	18.18	14.55	4.00
42. 2.75 „	12.80	25.45	21.82	21.82	21.82	4.35
43. 2.75 „	13.80	25.45	25.45	23.62	21.82	4.00

Helix aspersa (cont.).

Mature Forms.

Length of shell.	Breadth of cerebral ganglion. Per cent.	Cerebro-pleural connectives.		Cerebro-pedal connectives.		Length of visceral chain. Per cent.
		Left. Per cent.	Right. Per cent.	Left. Per cent.	Right. Per cent.	
44. 2.80 cm.	12.50	16.08	16.08	14.30	16.08	3.57
45. 2.80 "	12.50	23.23	21.45	25.00	23.23	3.58
46. 2.85 "	10.53	19.30	15.80	15.80	15.80	5.27
47. 2.90 "	8.63	12.08	13.80	12.08	12.08	4.48
48. 2.90 "	11.05	17.25	13.80	13.80	13.80	4.18
49. 2.95 "	13.30	23.75	20.35	20.35	16.98	3.39
50. 3.10 "	9.65	19.36	16.15	16.15	16.15	3.87

Placostylus bivaricosus.

Mature Forms.

1. 5.15 cm.	7.76	11.72	10.06	9.75	9.75	2.72
2. 5.60 "	6.25	12.50	9.81	10.07	8.92	1.97
3. 5.80 "	5.54	11.19	9.45	11.19	10.04	1.88
4. 5.80 "	5.69	10.35	9.45	8.62	8.62	2.47
5. 5.80 "	5.71	9.46	8.65	9.46	8.65	2.24
6. 5.90 "	6.45	11.88	11.02	11.02	9.34	2.08
7. 6.00 "	5.87	13.35	11.68	11.68	10.09	2.24
8. 6.10 "	5.12	9.02	8.30	9.03	8.20	2.05
9. 6.10 "	5.55	9.02	8.19	8.19	7.36	2.06
10. 6.50 "	4.48	12.30	11.54	10.00	9.25	2.15
11. 6.60 "	5.30	10.06	8.84	9.06	9.06	2.86
12. 7.10 "	5.35	12.68	10.56	9.15	8.45	1.55
13. 7.30 "	4.66	9.59	6.85	10.28	8.25	1.51
14. 7.50 "	3.60	7.99	7.99	7.35	7.35	1.93

Macrochlamys versica.

Mature Forms.

1. .50 cm.	.0200	.0020	.0020	.0040	.0040	.040
2. .50 "	.0280	.0040	.0020	.0060	.0060	.050
3. .65 "	.0169	.0038	.0038	.0046	.0046	.037
4. .65 "	.0169	.0038	.0038	.0062	.0046	.040
5. .70 "	.0170	.0028	.0028	.0057	.0043	.037
6. .75 "	.0160	.0026	.0026	.0040	.0040	.035
7. .75 "	.0160	.0026	.0026	.0040	.0040	.035
8. .75 "	.0160	.0026	.0026	.0053	.0040	.036
9. .85 "	.0150	.0025	.0025	.0037	.0037	.030
10. .75 "	.0190	.0040	.0026	.0053	.0053	.035
11. .80 "	.0140	.0025	.0025	.0063	.0050	.035
12. .80 "	.0150	.0025	.0025	.0045	.0037	.034
13. .80 "	.0150	.0025	.0025	.0045	.0037	.030

Macrochlamys versica (cont.).

Mature Forms.

	Length of shell.	Breadth of cerebral ganglion. Per cent.	Cerebro-pleural connectives.		Cerebro-pedal connectives.		Length of visceral chain. Per cent.
			Left.	Right.	Left.	Right.	
14.	.80 cm.	.016	.0037	.0025	.0075	.0063	.035
15.	.80 "	.018	.0025	.0025	.0037	.0037	.033
16.	.80 "	.018	.0025	.0025	.0037	.0037	.034
17.	.80 "	.018	.0025	.0025	.0063	.0050	.034
18.	.80 "	.018	.0025	.0025	.0063	.0063	.035
19.	.80 "	.018	.0050	.0050	.0050	.0075	.033
20.	.85 "	.014	.0024	.0024	.0035	.0035	.032
21.	.85 "	.018	.0035	.0035	.0059	.0059	.033
22.	.85 "	.018	.0035	.0035	.0071	.0059	.035
23.	.90 "	.013	.0022	.0022	.0045	.0055	.025
24.	.90 "	.013	.0022	.0022	.0055	.0045	.030
25.	.90 "	.016	.0022	.0022	.0055	.0045	.029

Limnæa stagnalis.

1.	2.55 cm.	11.77	.790	.790	.460	.460	17.40
2.	2.60 "	10.00	.770	.770	.380	.380	15.80
3.	2.60 "	11.55	.960	.960	.380	.380	14.15
4.	2.75 "	10.55	.730	.730	.370	.370	17.10
5.	2.75 "	10.90	.730	.730	.370	.370	16.75
6.	2.80 "	10.70	.720	.720	.350	.350	16.10
7.	2.85 "	8.80	.700	.700	.420	.420	17.60
8.	2.85 "	14.05	.700	.700	.520	.520	17.40
9.	2.90 "	12.10	.690	.690	.510	.510	17.90
10.	2.95 "	10.02	.680	.680	.340	.410	17.00
11.	3.00 "	8.35	.670	.670	.330	.330	15.05
12.	3.00 "	8.67	.835	.835	.500	.470	13.34
13.	3.00 "	10.06	.670	.670	.500	.500	13.34
14.	3.00 "	10.06	.670	.830	.500	.330	16.60
15.	3.10 "	9.68	.650	.650	.475	.475	16.75
16.	3.10 "	9.63	.810	.650	.475	.388	12.80
17.	3.10 "	9.68	.650	.650	.388	.388	8.38
18.	3.10 "	11.30	.810	.810	.325	.485	15.60
19.	3.15 "	8.55	.795	.795	.380	.380	14.60
20.	3.15 "	9.50	.635	.635	.318	.318	15.20
21.	3.20 "	9.40	.780	.780	.470	.470	15.75
22.	3.20 "	10.90	.635	.635	.312	.312	14.15
23.	3.20 "	12.50	.635	.635	.312	.312	15.60
24.	3.25 "	12.30	.770	.770	.460	.460	15.40
25.	3.25 "	10.45	.595	.595	.445	.445	16.90

The relevance of the data in the table on the previous pages to the problems under consideration may be explained as follows:—I wished to ascertain (1) whether the eight types of Pulmonate Nervous System were distinct from one another, or whether grading from one type into another might occur; (2) whether confusion of types might not have arisen by description of immature individuals with incompletely concentrated nervous systems.

I have determined the mean value for each set of measurements taken, together with the standard deviation and the probable error. The value of the last is in every case large because the total number of specimens examined is somewhat small; but an expert statistician assures me that it is never so large as to invalidate my conclusions. Distinctness of type depends on the significance of the difference between two means. This is determined statistically by the use of the following formula * :—

$$\text{P.E.} = \sqrt{E_1^2 + E_2^2},$$

where P.E. = probable error of the difference between two means,

$$\begin{array}{llll} E_1 = & \text{,,} & \text{,,} & \text{1st mean M. 1,} \\ E_2 = & \text{,,} & \text{,,} & \text{2nd ,, M. 2.} \end{array}$$

If the difference between M_1 and M_2 is less than three times the probable error of their differences, distinctness of type could not be inferred from the measurements taken.

The differences of the means, and the probable errors of their differences are given in the table opposite, and it will be seen that in no case is there any confusion of type, nor of the immature and mature forms, since the value for P.E. does not exceed one third of the value of the difference between means.

There is, of course, considerable variation, but it is not great enough to suggest that the ganglia may be fused at one stage of development or widely separated at another, either in (1) young or old specimens, or (2) individuals of the same age.

The actual measurements show that the nervous system is a precocious development in those specimens in which immature and mature forms were found. (The development of a lip, if it occurred, or the hardening of the edge of the shell aperture were taken as criteria of maturity.) The growth of the body and shell proceeds at a greater rate than does that of the ganglionic masses, which appear to be fully developed early in the Pulmonate life-history. This makes it improbable that the description of immature forms may have led to confusion of types. The fact that the amount of connective tissue covering the whole nervous system is subject to great variation seems much more likely to lead to wrong descriptions of types, for

* See Babcock and Clausen, 'Genetics in relation to Agriculture,' 1918, p. 47.

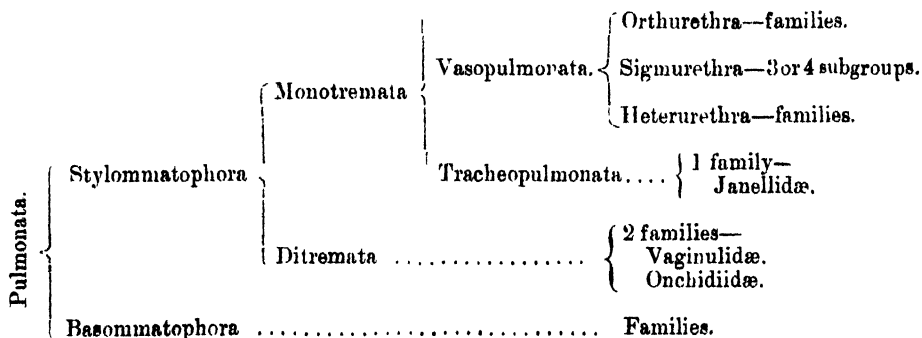
in a spirit-preserved specimen it is often extremely difficult to dissect away. In some mature specimens of *Helix aspersa* it was found to be very thick, while in others it hardly masked the ganglia at all.

The difficulty met with in dealing with this side of the subject lay in the scarcity of large numbers of specimens of a particular type, and I was consequently unable to examine examples of all the eight types of nervous system, or even a number of more than one member of a single type, intensively. It is, of course, possible that descriptions based on examination of a single specimen might lead to error, since complete condensation of the nervous system might not yet have taken place, but, as a general rule, it seems likely that this contingency is avoided by the early development of the ganglia.

VII. CLASSIFICATION OF THE PULMONATA.

I have included a table of the classification of the Pulmonata at this stage, in order that the position of the specimens, described in the next section, can be clearly appreciated.

In the classification of the Pulmonata, set forth by Pilsbry (1900), this group is subdivided as follows:—



This general scheme is based on considerations of the morphological characters of the following structures, which Pilsbry (1894) regarded as being of primary importance:—

Organs of protection (shell, mantle, and integument of the body).

„ locomotion (foot, with pedal grooves, tail-gland, etc.).

„ reproduction (genitalia, comparative size of eggs, etc.).

„ nutrition (jaw, teeth, intestinal tract, kidney).

Nervous system (including sense-organs, such as tentacles).

Muscular system.

The Vasopulmonate groups of the Heterurethra and Orthurethra do not exhibit very diverse characters, but the Sigmurethra are further subdivided into Holopoda, Aulacopoda, Agnatha, and Agnathomorpha. The affinities of the last three subgroups have been investigated by Watson (1915). The relationships of the Holopoda are still not completely understood, though Watson (1919, 1920, 1923) and others have contributed towards a clearer understanding of the classification. I have confined my practical investigations to the Sigmurethra. It will be seen from examination of Table I (p. 48) that the greatest variation in the type of nervous system occurs in this group.

As the families belonging to the three subgroups of the Vasopulmonata are very numerous, I include a list of them here for the sake of clearness :—

Vasopulmonata	Orthurethra	Subdivisions, if any, to be determined.	Valloniidæ.
			Enidæ.
			Pupillidæ.
			Punctidæ.
			Pertulidæ.
			Ferussacidæ.
			Amastriidæ.
	Sigmurethra	Holopoda	Helicidæ.
			Acavidæ.
			Bulimulidæ.
			Cerionidæ.
			Urocoptidæ.
			Megaspiridæ.
			Clausiliidæ.
		Agnathomorpha	Achatinidæ.
			Streptaxidæ.
			Circinariidæ.
			Aperidæ.
			Rhytididæ.
Agnatha	{	Oleacinidæ.	
		Testacellidæ.	
		Trigonochlamydæ.	
		Zonitidæ.	
		Limacidæ.	
Aulacopoda	{	Endodontidæ.	
		Laomidæ.	
		Arionidæ.	
		Philomycidæ.	
		Succineidæ.	
Heterurethra	Elasmognatha	Succineidæ.	

VIII. DETAILED DESCRIPTIONS OF PULMONATE NERVOUS SYSTEMS, ARRANGED ACCORDING TO TYPE.

1. Basommatophoran type.

Under this heading are included most of the Basommatophora, and the members of the family Clausiliidæ, among the Stylommatophora.

A. BASOMMATOPHORA.

i. ELLOBIIDÆ.

E. g., *Auricula myosotis* (Pl. 1. fig. 4). (*Pelseneer*, 1893. p. 74.)—The cerebral ganglia are oval in shape, and the commissure is about equal in length to the greatest breadth of the ganglia. The cerebro-pleural and cerebro-pedal connectives are long, the right cerebro-pleural connective being about half the length of the left. The right pleuro-pedal connective is twice as long as the left. The variation in the length of the connectives causes the visceral chain to be asymmetrical in appearance. The five ganglia are separated from one another by lengths of visceral commissure. The left pleural and parietal (subintestinal) ganglia lie close together; the abdominal ganglion is equidistant from both parietals; the right parietal (supra-intestinal) ganglion is separated by a considerable length of commissure from the right pleural ganglion. *Pelseneer* described and figured four visceral nerves, two from the abdominal ganglion, "aux organes génitaux," and two pallial nerves from the parietal ganglia.

E. g., *Carychium minimum* (Pl. 1. fig. 6). (*Simroth*, 1910.)—The cerebral ganglia are oval in shape and the commissure is very short. The cerebro-pedal connectives are twice as long as the cerebro-pleural connectives. The pedal ganglia are fairly widely separated, and *Simroth* figures one pedal commissure. The visceral chain consists of five ganglia joined to one another by lengths of visceral commissure. The parietal ganglia are widely separated from the pleural ganglia, but are nearer to the abdominal ganglion, particularly on the right side. According to the figure the right parietal ganglion is three times as large as the left. The left parietal ganglion gives off one nerve, the abdominal ganglion two nerves, and the right parietal ganglion two nerves, but their destination is not described.

E. g., *Marinula juanensis* (Pl. 1. fig. 7). (*Odhner*, 1925.)—This nervous system has already been described (see p. 10).

ii. AMPHIROLIDÆ.

E. g., *Amphibola nuxavellana* (Pl. 1. fig. 5). (*Pelseneer*, 1893, p. 78.)—The nervous system appears more concentrated in this genus, owing to the short cerebro-pleural and cerebro-pedal connectives. The cerebral ganglia are oval in shape, and the commissure is about one and a half times the breadth of the ganglia. The pedal commissure is long, the pleuro-pedal connectives are very short. There are five ganglia in the visceral chain, joined by lengths of commissure. The pleural and parietal (sub-intestinal) ganglia lie close together on the left side, but are more widely separated on the right. The abdominal ganglion is slightly nearer the right parietal than the left. The left parietal ganglion gives off one pallial nerve; the right parietal two, one of which innervates the osphradium. The abdominal ganglion gives off two nerves, “aux viscéraux principaux,” and one which apparently arises from the commissure on the right, where it joins the ganglion. Its destination is not described.

iii. OTINIDÆ.

E. g., *Otina otis*. (*Pelseneer*, 1900.)—The cerebral ganglia are joined by a long commissure and have a marked external lateral lobe. The cerebro-pedal connectives are of moderate length; the cerebro-pleural connectives are not apparent, as the pleural ganglia are closely applied to the cerebrals. (*Cf.* the fusion of the cerebral and pleural ganglia in the Prosobranchia. This is an unusual occurrence in the Pulmonata.) The right parietal ganglion is separated by a short length of commissure from the right pleural, and by a long stretch from the abdominal ganglion. The left parietal ganglion is adjacent to the left pleural, but widely separated from the abdominal ganglion. *Pelseneer* figures three visceral nerves, one from the right parietal ganglion to the mantle, and two from the abdominal ganglion, one genital and one pallial nerve.

iv. LIMNÆIDÆ.

E. g., *Limnæa stagnalis* (Pl. 1. fig. 9). (*Lacaze-Duthiers*, 1872 A.)—The cerebral ganglia are distinctly lobed, and are joined by a fairly long commissure. *Lacaze-Duthiers* figures what he calls the “nerf satellite des artères labiales,” and which probably corresponds to the subcerebral commissure of the Stylomatophora. The cerebro-pedal connectives are very short. The pedal ganglia are large, and are joined by three commissures, the third being most posterior and having the appearance of a very thin nerve, and giving rise to a fine median nerve to the pedal groove. Three commissures have not been reported by any other workers, and it seems likely that the last one is one of the branching pedal nerves. I did not find anything like

this in the specimens of *Limnæa* which I examined. The visceral chain consists of five ganglia, all separated from one another by short lengths of commissure. No nerves originate from the pleural ganglia; but Lacaze-Duthiers figures one arising from the left parietal ganglia, the *left pallial nerve*, and two arising from the right parietal ganglion, the *anterior pallial nerve* to the respiratory region of the mantle, and the *right pallial nerve* to the respiratory aperture and osphradium. The abdominal ganglion gives rise to four nerves which originate from right to left as follows: an *aortic nerve*, a *genital nerve*, and two *pallial nerves*.

E. g., *Amphipeplea glutinosa*.—(V. Jhering, 1877.)—The nervous system resembles that of *Limnæa*, except that the right parietal ganglion is considerably larger than the left.

B. STYLOMMATOPHORA. **Sigmurethra.** Holopoda.

i. CLAUSILIIDÆ.

E. g., *Balea perversa* (Pl. 4. fig. 46).—Simroth (1910) instances this form of nervous system as being typical of many Stylommatophora, but it should rather be regarded as being a primitive character, since it is the type met with in the Basommatophora, and is not frequent in occurrence in the groups of more specialized Pulmonates.

In *Balea*, the cerebral ganglia are lobed and the commissure is very long. The connectives are also long, particularly the cerebro-pedal connective. The pedal ganglia approximate in the middle line, and are joined to the pleural ganglia by fairly long connectives. The right parietal ganglion is smaller than the left, and is more widely separated from the right pleural ganglion than its fellow is from the left pleural ganglion. The abdominal and left parietal ganglion almost touch each other. Simroth figures one nerve arising from each parietal ganglion and two from the abdominal ganglion, but does not describe their distribution.

E. g., *Clausilia ventricosa*.—Simroth (1910, p. 255) mentions that the nervous system of *Clausilia* has a visceral chain "mit fünf gut getrennten Ganglion," but he does not figure or describe it fully. Wiegmann (1878) gives an account of *Clausilia reiniana* and a lateral view of the nervous system which is very confusing. V. Jhering (1877, pp. 237–38) described the nervous system of *Clausilia ventricosa*. The cerebral commissure is broad and fairly long, and the posterior region of the cerebral ganglia is large in comparison with the rest. The pedal ganglia approximate in the middle line, and the cerebro-pedal connectives are fairly short. The visceral

ganglia are all separated from one another. The pleural (commissural) ganglia lie near the pedal ganglia, but the other ganglia of the visceral chain lie far behind the pedal ganglia. The longest part of the visceral commissure is between the left pleural and left parietal (pallial) ganglia; the corresponding length of commissure on the right side is only half as long. "Dadurch kommt es, dass das Genitalganglion und das durch eine kurze Commissur mit ihm verbundene linke Pallialganglion weit hinten zur Seite der Mittellinie symmetrisch gelegen sind." This statement of v. Jhering is rather ambiguous and might be taken to mean either of two alternatives: (1) the abdominal (genital) ganglion lies on one side of the middle line, with the left parietal (pallial) ganglion symmetrically disposed opposite it, or (2) that both the abdominal and left parietal ganglia lie on one side of the middle line, as in *Balea* (Pl. 4. fig. 46). Fortunately, this ambiguity is made clear by Wiegmann's (1894) figure of *Clausilia obesa*, which shows distinctly that in this species the latter alternative is the case, the left parietal ganglion lying asymmetrically with the abdominal ganglion.

ii. ACHATINIDÆ. STENOGYRINÆ.

E. g., *Stenogyra decollata* (Pl. 4. figs. 47 & 48).—Simroth (1910, p. 255) mentions that the visceral chain of *Stenogyra* consists of five visceral ganglia, all separated from one another, but does not give a description or a diagram.

V. Jhering (1877) described and figured the nervous system of *Stenogyra decollata* (Pl. 4. fig. 47). The cerebral ganglia exhibit three distinct lobes and are united by a broad, fairly short commissure. The cerebro-pleural and cerebro-pedal connectives are long. The pedal ganglia approximate in the middle line, and there are distinct connectives to the pleural ganglia, which are separated from the other ganglia of the visceral chain by short lengths of visceral commissure. V. Jhering figures two parietal ganglia on the left side joined by a short commissure. The other visceral ganglia are adjacent to one another, but quite distinct. The accessory parietal ganglion brings the number in the visceral chain up to six. The innervation from these ganglia is as follows: the pleural ganglia give off no nerves; the right parietal ganglion gives off one *pallial nerve* to the respiratory aperture; the abdominal ganglion gives off one nerve to the right half of the mantle and one to the genital organs; the 2nd left parietal ganglion gives off one nerve to the centre and right half of the mantle; the 1st left parietal ganglion gives off one nerve to the left half of the mantle. V. Jhering regards the accessory (2nd) parietal ganglion and the abdominal ganglion, together, as being homologous with the abdominal ganglion of *Helix*.

Re-investigation of this nervous system (Pl. 4. fig. 48) does not confirm the presence of this 6th visceral ganglion. The pleural ganglia are separated from the parietal and abdominal ganglia by short commissures,

these last three ganglia being adjacent to one another but quite distinctly discernible. The whole nervous system is thickly covered with connective-tissue, which may account for the differences between Simroth's and v. Jhering's descriptions.

In *Stenogyra octona* (Wiegmann, 1894) the visceral ganglia are rather more separated, the right pleural ganglion being connected by a length of commissure to the right parietal, and the left parietal ganglion being less closely applied to the abdominal.

Hence it appears that *Stenogyra* has a nervous system intermediate between Types I and II, though possibly nearer to Type II, since some of the ganglia are adjacent to one another. I have included it in Type II in Table I, but it is not a typical example of the Zonitoid type of nervous system.

2. Zonitoid type.

Under this heading are included members of three Basommatophoran families—the Planorbidae, Physidae, and Ancyliidae, and members of the Stylommatophoran families—Enidae, Helicidae, Eulotidae, Achatinidae, Urocoptidae, Bulimulidae, Cerionidae, Testacellidae, Zonitidae, Arionidae, Oleacinidae, Rhytididae.

A. BASOMMATOPHORA.

i. PLANORBIDÆ.

E. g., *Isidora (Physopsis) globosa* (Pl. 1. fig. 10). (Connolly & Watson).—The cerebral ganglia are large and oval in shape, and united by a fairly long, broad commissure. The cerebro-pleural and cerebro-pedal connectives are so short as to be almost non-existent. Consequently the nervous system appears very concentrated and lies behind the buccal mass. The visceral ganglia are five in number, all adjacent, but all quite different.

E. g., *Planorbis pfeifferi* (Connolly & Watson) has a nervous system closely resembling that of *Isidora*—the number and distribution of the visceral nerves is given in neither genus.

ii. PHYSIDÆ.

E. g., *Physa acuta* (Pl. 1. fig. 8).—Iacaze-Duthiers (1872 A) states that the nervous system of *Physa* resembles that of *Limnea* in every way, except that he could not find the "nerf aux artères labiales," and that the visceral chain is inverted, the animal being a sinistrally-coiled Pulmonate. His figures do not confirm this statement of resemblance, however (cf. Pl. 1. figs. 8 & 9), the visceral chain being more concentrated in *Physa*, as the visceral commissure has disappeared. Connolly and Watson draw attention

to the resemblance between the nervous systems of *Physa* and *Isidora*, and *Physa* should evidently be included as a Zonitoid type.

iii. ANCYLIDÆ.

E. g., *Ancylus capuloides*.—Aeberhardt (1903) described and figured the nervous system of this Pulmonate. It is more concentrated than that of *Isidora*, the commissures and connectives being very short. There are five distinct ganglia in the visceral chain.

B. STYLOMMATOPHORA.

I. Orthurethra.

i. ENIDÆ.

E. g., *Conulinus junodi* (Pl. 2. fig. 15). (*Comolloy & Watson*, p. 155.)—‘The nerve-ring is small and surrounds the œsophagus, salivary ducts, and buccal retractor. . . . The large cerebral ganglia are united by a fairly short, but rather narrow, arched cerebral commissure. . . . The pedal ganglia . . . lie close together, and each is obscurely divided by a slight dorsal furrow into a large anterior and a smaller posterior portion. The anterior portions are united by a broad anterior pedal commissure, and bear on their upper sides the otocysts. The posterior portions are united by the narrower posterior commissure. The cerebro-pleural connectives are relatively short and the visceral ganglia are closely aggregated and somewhat compressed laterally, although they are quite distinct from one another, as may be seen from the figure. The right parietal ganglion is . . . much larger than the left.’

II. Sigmurethra. (a) Holopoda.

i. HELICIDÆ. 1. POLYGYRINÆ.

E. g., *Solaropsis* sp. (Pl. 2. fig. 18).—The cerebral ganglia are very distinctly lobed, and the commissure is about equal in length to the greatest breadth of the ganglia. The cerebro-pleural and cerebro-pedal connectives are of moderate length. The pedal and visceral ganglia are closely covered with a sheath of connective tissue; when this is removed they are seen to be closely aggregated, so that the pedal commissures and pleuro-pedal connectives cannot be distinguished. The five ganglia of the visceral chain are quite distinct. The pleural ganglia do not give off any nerves. Two pallial nerves arise from the two parietal ganglia, and the anal and genital nerves arise from the abdominal ganglion.

2. CAMÆNINÆ.

E. g., *Camæna senegalensis* (Pl. 2. fig. 19).—The cerebral ganglia form a confused mass, and are thickly covered with connective tissue, which it is impossible to dissect away without injuring the ganglia themselves. The cerebro-pleural and cerebro-pedal connectives are short, and hence the nerve-ring is small. The connective-tissue sheath also covers the pedal and visceral ganglia, but, on removing this, short pleuro-pedal connectives can be seen. The pedal ganglia approximate in the middle line. There are five visceral ganglia, very closely aggregated, but quite distinct from one another.

E. g., *Amphidromus atricallosus* (Pl. 2. fig. 20).—The cerebral ganglia touch one another in the middle line, so that no commissure is apparent. The cerebro-pleural and cerebro-pedal connectives are of moderate length, the former being slightly longer than the latter, so that the visceral chain lies behind the pedal ganglia, which are adjacent in the middle line. The five visceral ganglia are all close together, but quite distinct.

Wiegmann (1894), working on *Amphidromus adamsi*, describes and figures a very similar nervous system.

3. HELICINÆ.

E. g., *Oreohelix cooperi* (Pl. 2. fig. 26).—The cerebral ganglia are oval, and are united by a very short, broad commissure. The cerebro-pleural and cerebro-pedal connectives are of moderate length, the cerebro-pleural connectives being the longer, so that the visceral chain lies behind the pedal ganglia. These are adjacent to one another in the middle line. The pleuro-pedal connectives are short but distinct. The five visceral ganglia are all separate, the abdominal ganglia being much the largest.

E. g., *Hadra argillacea*. (Wiegmann, 1894.)—The cerebral ganglia are oval and joined by a short, broad commissure. The cerebro-pleural and cerebro-pedal connectives are fairly short. The pedal ganglia approximate in the middle line, and the pleuro-pedal connectives are short. The visceral ganglia are very closely aggregated, but it is possible to distinguish five components. Wiegmann mentions two pairs of small nerves from the pleural ganglia, which anastomose with the cerebro-buccal connectives, to which innervate part of the retractor pharyngeal muscles. Two other pairs of small pleural nerves pass to the retractor muscles of the smaller tentacles. The parietal ganglia give off two large pallial nerves. The abdominal ganglion gives off three nerves—one on the right to the region anterior to the pulmonary orifice, the central one to the genitalia, and the one on the left to the tail retractor(?).

E. g., *Euparypha pisana* (Pl. 3. fig. 39).—The cerebral ganglia are oval in shape, and are joined by a broad commissure of moderate length. The cerebro-pleural and cerebro-pedal connectives are of moderate length. The pedal ganglia approximate in the middle line. The five ganglia of the visceral chain are all distinct. The left parietal ganglion gives off one pallial nerve; the abdominal ganglion gives off a cutaneous pallial, an anal, and an intestinal nerve. The right parietal ganglion gives off two pallial nerves.

ii. EULOTIDÆ.

E. g., *Eulota similis* (Pl. 2. fig. 27).—There is very little connective tissue wrapping round the nervous system in this species. The cerebral ganglia are oval and united by a very short, broad commissure. The cerebro-pleural and cerebro-pedal connectives are of moderate length, and the visceral and pedal ganglia are much compressed. Five divisions can be distinguished in the visceral mass.

iii. BULIMULIDÆ. ORTHALICINÆ.

E. g., *Orthalicus zebra* (Pl. 3. fig. 37).—The cerebral ganglia are distinctly trilobed and touch one another in the middle line. The cerebro-pleural and cerebro-pedal connectives are slender and of moderate length. The pedal ganglia are joined by a short commissure, and, instead of lying beneath or in front of the visceral mass, they lie above and at right angles to it. The visceral ganglia are much compressed, but five divisions can be distinguished. There are no pleural nerves. The left parietal ganglion gives off a pallial nerve I: the abdominal ganglion gives off three nerves; III, cutaneous pallial; IV, intestinal; V, anal: the right parietal ganglion gives off one pallial nerve II, which soon branches into two.

E. g., *Oxystyla bensoni* (Pl. 3. fig. 38).—This nervous system is very like that of *Orthalicus zebra*, except that the pedal ganglia lie behind the visceral mass; no pedal commissure is apparent.

iv. CERIONIDÆ.

E. g., *Cerion* sp. (Pl. 3. fig. 41).—The cerebral ganglia are oval in shape and united by a very short commissure. The cerebro-pleural and cerebro-pedal connectives are of moderate length, the latter being longer than the former. The pedal ganglia are adjacent to one another in the middle line. The pleuro-pedal connectives are of moderate length. The left parietal ganglion is separated by a short length of visceral commissure from the left pleural ganglion, but the other ganglia of the visceral chain are all adjacent. The right parietal ganglion is as large as the abdominal ganglion and two and a half times as large as the left parietal ganglion.

This is another example of a rather dubious type of nervous system, and again it appears intermediate between Type I and Type II.

V. UROCOPTIDÆ. UROCOPTINÆ.

E. g., *Brachypodella agnesiana* (Pl. 3. fig. 42). (*Pilsbry*, 1904.)—The cerebral ganglia are oval, and are joined by a short, broad commissure. The cerebro-pedal connectives are half as long as the cerebro-pleural connectives, so that the visceral chain is posterior to the pedal mass. The pedal ganglia are joined by a short commissure. The pleuro-pedal connectives are of moderate length. The five ganglia of the visceral chain are all adjacent to one another, except the right parietal ganglion, which is separated by a very short commissure from the right pleural ganglion. The left parietal ganglion is about twice as large as the right parietal ganglion.

E. g., *Brachypodella brucciidi* (Pl. 3. fig. 43).—The cerebral ganglia are oval and adjacent to one another in the middle line. The cerebro-pleural and cerebro-pedal connectives are of moderate length, the former being longer than the latter, with the result that the visceral chain lies behind the pedal ganglia, which are joined together in the middle line. The pleuro-pedal connectives are short. The pleural ganglia are separated by short commissures from the other three ganglia of the visceral chain; the parietal and abdominal ganglia are closely aggregated together, but can be seen to be distinct from one another.

These two species of *Brachypodella* are also intermediate types between Type I and Type II.

VI. ACHATINIDÆ. 1. STENOGYRINÆ.

E. g., *Pseudoglossula cressyi* (Pl. 4. fig. 49) and *P. boivini*. (*Connolly & Watson*.)—The cerebral ganglia are slightly lobed, and are joined by a commissure of moderate length. The cerebro-pleural and cerebro-pedal connectives are very long and slender. The pedal ganglia are adjacent to one another in the middle line and lie anteriorly to the visceral chain. The pleuro-pedal connectives are short but distinct. The five visceral ganglia are rather closely approximated, but not completely united.

2. ACHATININÆ.

E. g., *Burtoa arnoldi* (Pl. 4. fig. 52).—The nervous system is covered with a thick sheet of connective tissue which completely masks the contours of the ganglia, and which adheres so closely to the cerebral ganglia that it is impossible to free them from it. The cerebro-pleural and cerebro-pedal connectives are short. The pedal ganglia are joined in the middle line. The five ganglia of the visceral chain are quite distinct from one another, although

all adjacent. The connective tissue covers the nerves as well as the ganglia, and their origin and number are difficult to determine. The left parietal ganglion gives off two pallial nerves; the abdominal ganglion gives off three nerves—cutaneous pallial, anal, and intestinal; and the right parietal ganglion gives off one pallial nerve.

E. g., *Achatina fulica* (Pl. 4. fig. 51).—The nervous system is closely and thickly covered by a sheath of connective tissue, with which the anterior musculature is intimately related. The cerebral ganglia are oval and adjacent to one another in the middle line. The cerebro-pleural and cerebro-pedal connectives are of moderate length. The pedal ganglia approximate in the middle line, and the visceral ganglia are closely applied to them. The visceral chain is much compressed; the two pleural ganglia can be distinguished as being separate, also the right and left parietal ganglia, although these and the abdominal ganglion are closely applied to one another. Two pallial nerves arise from each parietal ganglion and three nerves from the abdominal ganglion—cutaneous pallial, anal, and intestinal.

E. g., *Achatina panthera*. (Wiegmann & V. Martens, 1898.)—The cerebral ganglia are joined by a short commissure. The cerebro-pleural and cerebro-pedal connectives are also fairly short. The pedal ganglia are adjacent to one another in the middle line, and the visceral chain lies behind them. There are five visceral ganglia, which are much compressed but still remain distinct.

(b) Agnatha.

i. TESTACELLIDÆ.

E. g., *Testacella fischeriana* (Pl. 4. fig. 54).—This nervous system was described and figured by Plate (1891), and that of *T. haliotideæ* by v. Jhering (1877) and Moquin-Tandon (1885).

The cerebral ganglia are oval and joined by a short commissure in *Testacella fischeriana*. The cerebro-pleural and cerebro-pedal connectives are fairly short. The pedal ganglia touch one another in the middle line. The five ganglia of the visceral chain are all distinct, but adjacent to one another.

Moquin-Tandon's figure of *Testacella haliotideæ* is very like Plate's figure of *T. fischeriana*, except that the cerebral ganglia practically touch one another in the middle line, the commissure being apparent only on their posterior side. In v. Jhering's description of this species he mentions that the right pleural and parietal ganglia are separated by a short commissure. This is not confirmed by Moquin-Tandon's figure.

In *Testacella maugei* (Lacaze-Duthiers, 1872 B) the cerebral ganglia touch in the middle line, but the cerebro-pleural and cerebro-pedal connectives are very long. The left pleural and parietal ganglia are adjacent, but the other

ganglia of the visceral chain are separated by short lengths of commissure. The pleuro-pedal connectives are short and the pedal ganglia approximate to one another.

The nervous systems of some species of *Testacella* are of an intermediate type—between Types I and II.

(c) **Aulacopoda.**

ii. **ZONITIDÆ.**

E. g., *Zonites cellarius* (Pl. 4. fig. 56). (*Lacaze-Duthiers*, 1872 B.)—This nervous system has already been described (on p. 15) as exemplifying the Zonitoid type. That of *Zonites algirus*, according to *Nabias* (1894), resembles that of *Zonites cellarius* very closely.

E. g., *Helicarion gomesianus* (Pl. 4. fig. 57). (*Watson*, 1920.)—The nerve-ring is too small to allow the buccal mass to be retracted through it. The cerebral ganglia lie on the sides of the œsophagus and have well-developed accessory lobes. "The cerebral commissure is broad and slightly arched, and a subcerebral commissure also appears to be present" (p. 94). The cerebro-pleural and cerebro-pedal connectives are shorter than is usual in the Zonitoid type of nervous system. The pedal ganglia are united by two short commissures, which do not show in *Watson's* diagram. The pleural, parietal, and abdominal ganglia are closely aggregated together, but are all distinguishable from one another, the right parietal ganglion being twice as large as the left.

E. g., *Ledoulxii mozambicensis* (Pl. 4. fig. 58). (*Connolly & Watson*.)—The nerve-ring is small and the cerebral ganglia have prominent lateral lobes. The cerebral commissure is very broad and of moderate length. The cerebro-pleural and cerebro-pedal connectives are short. The pedal ganglia approximate in the middle line. The visceral chain is asymmetrical, the five ganglia being all distinct from one another, though closely aggregated.

E. g., *Vitrina diaphana*. (*Aeberhardt*, 1903.)—There are five ganglia in the visceral chain. The cerebro-pleural and cerebro-pedal connectives and the cerebral commissure are much reduced, but the pleuro-pedal connectives and pedal commissure are still distinct.

E. g., *Machrochlamys boettgeri*. (*Wiegmann*, 1900.)—The cerebral ganglia touch one another in the middle line, so that no commissure is apparent. The cerebro-pleural and cerebro-pedal connectives are very short, the cerebro-pleural connectives being shorter on the left than on the right. The pedal ganglia approximate in the middle line. The pleuro-pedal connectives are very short. The left pleural ganglion is somewhat smaller than the right, the right parietal ganglion is much larger than the left. All the five ganglia are distinct from one another.

E. g., *Nanina nemorensis*. (Wiegmann, 1894.)—The nervous system is thickly covered with connective tissue and needs much dissection to free the ganglia. The cerebral ganglia are distinctly lobed and are joined by a short thick commissure. The cerebro-pleural and cerebro-pedal connectives are fairly short. The pedal ganglia approximate in the middle line. The pleuro-pedal connectives are short. All five ganglia in the visceral chain are distinct, although closely aggregated together. Wiegmann mentions, but does not figure, two nerves from the pleural ganglia to the retractor muscles of the smaller tentacles. Two pallial nerves arise from the parietal ganglion and three from the abdominal ganglion—the left to the tail retractor, the central one to the genital, the right a pallial nerve.

ii. ARIONIDÆ.

E. g., *Arion*.—The nervous system resembles that of *Zonites*, according to the description given by Nabias (1894).

iii. OLEACINIDÆ. iv. RHYTIDIDÆ.

According to Watson (1915), the nervous systems of the members of these two families generally are of the Zonitoid type.

3. Orthurethran type.

Under this heading are included members of the Orthurethran families Valloniidæ, Enidæ, Pupillidæ, Ferussacidæ, Partulidæ; of the Sigmurethran families Endodontidæ, Achatinidæ, Testacellidæ; and of the Heterurethran family Succineidæ.

I. Orthurethra.

i. VALLONIIDÆ.

E. g., *Vallonia costata* (Pl. 1. fig. 13). (Watson, 1920.)—The nervous system of this Pulmonate has been described on p. 15. The nervous systems of *Vallonia pulchella* and *V. excentrica*, and of *Acanthinula lamellata* and *A. aculeata*, are, according to Watson, almost identical with that of *Vallonia costata*.

E. g., *Patulastra balmei* (Pl. 1. fig. 14). (Watson, 1920.)—The visceral loop is "somewhat shorter [than in *Vallonia*], showing a tendency towards a greater concentration of the ganglia, but the nervous system remains of essentially the same type."

ii. ENIDÆ.

E. g., *Ena obscura*. (Watson, 1920.)—The nervous system is of the Orthurethran type.

iii. PUPILLIDÆ.

E. g., *Vertigo moulinsiana* and *V. antivertigo*, *Pyramidula rupestris*, and *Lauria cylindracea*. (Watson, 1920.)—The nervous systems are of the Orthurethran type.

iv. FERUSSACIDÆ.

E. g., *Cochlicopa lubrica* (Pl. 2. fig. 16). (Simroth, 1910.)—The cerebral ganglia are lobed, and are joined by a fairly long commissure. The cerebro-pedal connectives are long; the right pleuro-pedal connective is much shorter than the left, thus the visceral chain lies asymmetrically. The pleural ganglia are separated from the other visceral ganglia by short commissures. The right parietal ganglion is fused with the abdominal ganglion. Simroth figures one nerve arising from the left parietal ganglion and four nerves from the parieto-abdominal mass, but does not describe their distribution. Watson (1920) describes the nervous system of *Cochlicopa* as being identical with that of *Ena*, *Vertigo*, etc., in which case the visceral ganglia should be more concentrated than they appear from Simroth's figure.

v. PARTULIDÆ.

E. g., *Partula auriculata*. (V. Jhering, 1877.)—The cerebral commissure is short but distinct. The left cerebro-pleural connective is longer than the right, giving the visceral chain an asymmetrical appearance. The pedal ganglia are fused in the middle line. The right parietal ganglion is fused with the abdominal ganglion. No visceral nerves are figured or described.

II. Sigmurethra.

i. ENDODONTIDÆ.

E. g., *Patula rotundata* (Pl. 2. fig. 17). (Simroth, 1910.)—The cerebral ganglia show a lateral lobe and are joined by a moderate commissure. The cerebro-pedal connectives are long; the cerebro-pleural connectives are short. The pedal ganglia approximate in the middle line. The pleuro-pedal connectives are long. The left pleural and parietal ganglia are adjacent to one another; the right parietal ganglion is fused with the abdominal, and the fused mass is separated by a length of commissure from the right pleural ganglion. Simroth figures one nerve arising from the left parietal ganglion, and four arising from the parieto-abdominal ganglion, but does not describe their distribution.

E. g., *Goniodiscus rotundatus*.—Watson (1920, p. 8) mentions that in the nervous system of this genus the "abdominal ganglion tends to be united with the right parietal ganglion."

ii. ACHATINIDÆ. STENOGYRINÆ.

E. g., *Subuliniscus chiradzulensis* (Pl. 4. fig. 50). (Connolly & Watson, p. 180.)—"The cerebral ganglia are situated above the hind end of the buccal mass. They are broader than long, and are united by a rather thick commissure, the length of which is about equal to the breadth of each ganglion. . . . The cerebral ganglia are united with the pedal and pleural ganglia by two pairs of rather long connectives. As usual, the pedal ganglia are the largest in the ventral group, but the abdominal ganglion is also rather large. The right parietal ganglion, although much larger than the left, is smaller than the abdominal ganglion, with which it is somewhat closely united." The other ganglia of the visceral chain are separated from each other by lengths of commissure, and the pleuro-pedal connectives are long. Connolly and Watson figure one nerve arising from the parieto-abdominal mass, but do not describe its distribution.

iii. TESTACELLIDÆ.

E. g., *Daudebardia rufa* (Pl. 4. fig. 55). (Plate, 1891.)—The cerebral ganglia are oval, and are united by a commissure which is almost as long as the breadth of each ganglion. The cerebro-pleural and cerebro-pedal connectives are short. The pedal ganglia are the largest in the system. The visceral chain consists of four ganglia, the right parietal being fused with the abdominal ganglion. The parietal ganglion gives off a pallial nerve; the parieto-abdominal ganglion gives off five nerves to the viscera, mantle, and genitalia, although Plate was not able to trace them to their destinations.

The nervous system of *Daudebardia seulcyi* resembles that of *D. rufa* (Plate, 1891).

III. Heterurethra.

i. SUCCINIIDÆ.

E. g., *Omalonyx unguis* (Pl. 4. fig. 60). (Pelseneer, 1893.)—A figure of the nervous system is given, but no detailed description. The commissures and connectives are all very much reduced, so that the ganglia are closely concentrated together. In the visceral chain the right parietal is fused with the abdominal ganglion.

3. Heliciform type.

Under this heading are included members of the Stylommatophoran families Helicidæ, Urocoptidæ, Bulimulidæ, Aperiidæ.

i. HELICIDÆ. POLYGYRINÆ.

E. g., *Ashmunella cockerelli* (Pl. 2. fig. 21).—The cerebral ganglia are lobed, and are adjacent to one another in the middle line. The cerebro-pleural and cerebro-pedal connectives are long. The pedal ganglia are also adjacent to one another; the pleuro-pedal connectives are short but distinct. The pleural ganglia are separate from the parietal ganglion on the right side, and from the parieto-abdominal ganglion on the left side. The right parietal ganglion gives off two pallial nerves; the parieto-abdominal ganglion gives off four nerves—one pallial, one cutaneous pallial, one anal, one intestinal. Owing to the small size of the specimen, it was not possible to trace these to their destinations.

E. g., *Polygyra albolabris* (Pl. 2. fig. 22).—The cerebral ganglia are oval in shape, and are united by a very short commissure. The cerebro-pleural and cerebro-pedal connectives are shorter than those of *Ashmunella*. The pedal ganglia are adjacent to one another in the middle line. The visceral chain is compressed. The left parietal ganglion is fused with the abdominal ganglion. The innervation from these ganglia is as follows: right parietal ganglion, one pallial nerve I; parieto-abdominal ganglion, intestinal II, anal III, cutaneous pallial IV, left pallial V.

CAMÆNINÆ.

E. g., *Planispira surrecta* (Pl. 2. fig. 23). (Wiegmann, 1898.)—The cerebral ganglia are markedly lobed, and are united by a short commissure. The cerebro-pleural and cerebro-pedal connectives are of moderate length, and the pedal ganglia, which are adjacent to one another in the middle line, lie behind the visceral chain. The pleuro-pedal connectives are short. The pleural ganglia are closely applied to the right parietal, and to the parieto-abdominal ganglion on the left. The innervation is not given in detail, one nerve arising from the parietal ganglion and four from the parieto-abdominal ganglion being figured.

E. g., *Albersia pubiceps*. (Wiegmann, 1898.)—The cerebro-ganglia are joined by a very short commissure. The cerebro-pleural and cerebro-pedal connectives are of moderate length. The pedal ganglia approximate in the middle line. The visceral ganglia exhibit the typical heliciform arrangement, but are much concentrated. Wiegmann does not give the distribution of the visceral nerves.

E. g., *Papuina moseleyi* (Pl. 2. fig. 24).—The cerebral ganglia have distinct lateral lobe, and are joined by a fairly short commissure. The cerebro-pleural and cerebro-pedal connectives are of moderate length, the former being longer than the latter, with the result that the visceral chain lies behind the pedal ganglia, which approximate in the middle line. The pleural ganglia are closely applied to the right parietal ganglion and to the left parieto-abdominal ganglion. The innervation is as follows: (i) pallial nerve from the right parietal ganglion; from the parieto-abdominal ganglion, four nerves, pallial, pallial cutaneous, anal, intestinal.

HELICINÆ.

E. g., *Helix pomatia* (Pl. 2. fig. 25).—Many workers have described and figured *Helix pomatia* in great detail. Schmalz (1914) gave a very careful account of the nervous system, and his work was supplemented and corrected by Bang in 1917. Their results were confirmed by Kunze's histological investigations. The nervous system has been described on p. 16.

E. g., *Helix barbara*. (Rzymowska, 1914, p. 282).—The nervous system is typically heliciform. The cerebral ganglia are three-lobed and are joined by a commissure of moderate length. They are covered with a sheath of pigmented connective tissue. There are eight pairs of cerebral nerves, and an unpaired penis nerve on the right. Rzymowska did not describe the pair of cerebral arterial nerves which Kunze etc. found in *Helix pomatia*. The cerebro-pleural and cerebro-pedal connectives are of moderate length. The pedal ganglia are joined by two very short commissures. The visceral ganglia are four in number, the left parietal being fused with the abdominal ganglion, and the right parietal and pleural ganglia being not very distinct from one another. The parieto-abdominal ganglion gives off four nerves: (1) genital, (2) anterior pallial nerve, (3) cutaneous, (4) left pallial nerve. The left and right pleural ganglia do not give off any nerves. The right parietal ganglion gives off the right pallial nerve. In addition to six pairs of pedal nerves to the pedal muscles, Rzymowska describes six pairs of nerves, one pair to the columellar muscle and two pairs to the body-wall and genital organs. The origin of these nerves was not confirmed histologically, and it may be that the first pair, at any rate, may correspond to the pair recorded in *Helix pomatia*, as arising from the pleural ganglia.

E. g., *Helix nemoralis*.—V. Jhering (1877) mentions that the condition of fusion between the left parietal and abdominal ganglia met with in *Helix nemoralis* is characteristic of most Helicidæ.

E. g., *Sonorella walkeri*.—The cerebral ganglia are strap-shaped; this may be due to the connective tissue, which covers them very closely. The cerebro-pleural and cerebro-pedal connectives are of moderate length, and

the pedal ganglia approximate in the middle line. The visceral ganglia are closely aggregated together, and the left parietal is fused with the abdominal ganglion. The innervation is as follows: one pallial and two visceral nerves arise from the parieto-abdominal ganglion, and two pallial nerves arise from the right parietal ganglion. The specimen was too small to trace the distribution of these nerves.

E. g., *Euhadra eris*. (Wiegmann, 1900.)—The cerebro-ganglia are distinctly lobed, and are joined by a fairly long commissure. The cerebro-pleural and cerebro-pedal connectives are of moderate length, those on the right side being somewhat longer than those on the left. The pedal ganglia are adjacent in the middle line. The pleuro-pedal connectives are very short. The left parietal ganglion is fused with the abdominal ganglion. Wiegmann figures two nerves arising from the pleural ganglia, four from the parieto-abdominal ganglion, and one from the right parietal, but does not give their distribution.

E. g., *Helicella seetzeni* (Pl. 2. fig. 29).—The cerebral ganglia are slightly lobed and joined by a very short broad commissure. The cerebro-pleural and cerebro-pedal connectives are of moderate length, and the pedal ganglia approximate in the middle line. The visceral chain is condensed into an oval mass, which is closely applied to the pedal ganglia so that no pleuro-pedal connective is apparent. Four divisions can be distinguished in the visceral mass—pleural, parieto-abdominal, right parietal, and pleural ganglia. The innervation is as follows: one pallial, one cutaneous pallial, one anal, and one intestinal nerve from the parieto-abdominal ganglion. Two pallial nerves arise from the right parietal ganglion.

E. g., *Theba rotii* (Pl. 2. fig. 30).—The nervous system is covered with very little connective tissue. The cerebral ganglia are lobed, and are joined by a short commissure. The cerebro-pleural and cerebro-pedal connectives are of moderate length. A short pedal commissure can be distinguished. The four visceral ganglia are not as closely aggregated as in some other forms, e. g., *Helicella*. The innervation from the visceral ganglia is the same as in *Helicella*.

iii. UROCOTIDÆ.

E. g., *Eucalodium ghiesbreghtii* (Pl. 3. fig. 44). (Fischer & Crosse, 1878.)—The cerebral ganglia are lobed, and are joined by a very short commissure. The cerebro-pleural and cerebro-pedal connectives are long, the former being longer than the latter. The pedal ganglia approximate in the middle line. The left and right pleural ganglia are closely applied to the pedal ganglia. The left pleural ganglion is separated by a short length of commissure from the left parietal, which lies on the surface of the abdominal

ganglion, and is referred to by the authors as "un troisième à gauche, couche sur le ganglien sous-œsophagien postérieur, ou confondu avec lui." Fischer and Crosse figure two nerves from the pleural ganglia, four from the parieto-abdominal ganglion, and four from the right parietal ganglion, but do not describe their destinations.

E. g., *Berendtia taylori* (Pl. 3. fig. 45). (Fischer & Crosse, 1878.)—The cerebral and pedal ganglia closely resemble those of *Eucalodium*. The visceral chain is more concentrated, and evidently the left parietal ganglion is fused completely with the abdominal ganglion. Although the authors figure a fairly distinct right pleural ganglion, they state that they were unable to find one—"mais la commissure qui unit le ganglien sous-œsophagien antérieur [pedal ganglion] au ganglien postérieur [right parietal ganglion] est légèrement renflée, peut-être y découvrirait-on sur les exemplaires frais, un petit ganglien accolé."

iv. BULIMULIDÆ. BULIMINÆ.

E. g., *Placostylus bivaricosus* (Pl. 3. fig. 40).—The cerebral ganglia are lobed, and are joined by a fairly long commissure. The cerebro-pleural and cerebro-pedal connectives are long. The pedal ganglia approximate in the middle line. The pleuro-pedal connectives are very short but distinct. The left parietal ganglion is fused with the abdominal ganglion, and the fused mass gives off four visceral nerves—pallial, cutaneous pallial, anal, and intestinal. The right parietal ganglion is distinct and gives off two pallial nerves. The two pleural ganglia each give off one nerve to the retractor muscles of the buccal mass.

E. g., *Bulimulus interruptus* (Pl. 3. figs. 35 & 36).—The cerebral ganglia are oval, and are adjacent in the middle line. The cerebro-pleural and cerebro-pedal connectives are short. The pedal ganglia approximate in the middle line. The pleural ganglia are distinct, but the parieto-abdominal and right parietal ganglia are closely aggregated. Four nerves arise from the parieto-abdominal ganglion and two from the right parietal ganglion. I was unable to trace their distribution.

iv. APERIDÆ.

E. g., *Apera gibbonsi*. (Watson, 1915, p. 147.)—The cerebral ganglia are so closely bound together by connective tissue that they appear as one mass. There are two commissures, cerebral and subcerebral. The length of the cerebro-pleural and cerebro-pedal connectives varies with the size of the buccal mass. The pedal ganglia are the largest in the nervous system, and are joined by two commissures, pedal and para-pedal. "The pleural ganglia are less than half the size of the pedal ganglia." A very short length

of connective joins the left pleural to the parieto-abdominal ganglion, and the right parietal to the right pleural ganglion. A pair of nerves arise from the pleural ganglia to the body-wall (see pp. 12 and 13). The right parietal ganglion gives rise to a small pallial nerve. "The corresponding left pallial nerve is more slender, and arises from the outer or parietal part of the left visceral ganglion. This nerve innervates the left half of the mantle-cavity. From the median and abdominal portion of the left visceral ganglion two large nerves arise close together"—one to the anus and respiratory orifice and one to the pericardium and kidney.

5. *Hygromia* type.

Under this heading are included members of the Sigmurethran family Helicidæ.

i. HELICIDÆ. HELICINÆ.

E. g., *Hygromia limbata* (Pl. 3. fig. 31).—This nervous system has been described on p. 16.

E. g., *Ochtheiphila turricula* (Pl. 2. fig. 28). (Watson, 1923, p. 287).—The cerebral ganglia are united by a short commissure. The cerebro-pleural and cerebro-pedal connectives are of moderate length. The pedal ganglia are united in the middle line. The visceral chain, at first sight, seems to consist of a "single pair of pleuro-visceral ganglia. This appearance is due to the right parietal ganglion being completely fused with the right pleural ganglion on one side, and almost completely fused with the left pleural ganglion on the other." The left parietal ganglion is fused with the abdominal ganglion. Watson does not describe the visceral nerves.

6. *Ennea* type.

Under this heading are included members of the Sigmurethran families Streptaxidæ and Acavidæ.

AGNATHOMORPHA.

i. STREPTAXIDÆ.

E. g., *Ennea dussumieri* (Pl. 4. fig. 53).—This nervous system has been described on p. 16. According to Wiegmann and v. Martens (1898) the nervous system of *Streptaxis*, *Streptostele*, and *Priondiscus* are of this type.

HOLOPODA.

ii. ACAVIDÆ.

E. g., *Borus* sp. (Pl. 3. fig. 34).—The cerebral ganglia are slightly lobed and a commissure is just apparent. The cerebro-pleural and cerebro-pedal

connectives are long. The pedal ganglia are united in the middle line, and are closely applied to the visceral ganglia, which are three in number—two distinct pleural ganglia and a fused mass of parietal and abdominal ganglia, from which all the visceral nerves arise. The nervous system is closely and thickly covered with connective tissue, which is partially pigmented. The visceral nerves consist of two pallial nerves on the left, three visceral nerves (pallial cutaneous, anal, and intestinal) in the centre, and two pallial on the right.

E.g., *Ampelita xystera* (Pl. 3. fig. 33).—The cerebral ganglia are strap-shaped and no commissure is apparent, probably because the nervous system is thickly covered with connective tissue, which is impossible to dissect away. The cerebro-pleural and cerebro-pedal connectives are of moderate length. The pedal ganglia approximate in the middle line. Three components are distinguishable in the visceral mass—the visceral nerves (four in number, two pallial I & II, and two visceral II & III) arising from the central one, which consists of parietal and abdominal ganglia fused.

E.g., *Helicophanta sowerbyana* (Pl. 3. fig. 32).—The nervous system is covered with much connective tissue, and it is greatly condensed, the commissures and connectives being reduced, so that the whole forms a concentrated ring round the posterior region of the buccal mass. The pedal ganglia, which form a solid mass, lie slightly behind the visceral complex. The visceral ganglia are also completely fused together, but all the visceral nerves arise from the centre of the mass, suggesting that fusion has taken place primarily between the abdominal and parietal ganglia, and that, if the connective tissue could be removed, the pleural ganglia might still be distinguishable. The visceral nerves are similar from those of *Ampelita*.

E.g., *Acavus phoenix*.—Randles (1900) described the nervous system of *Acavus*, but did not give a figure, and his account is not very clear. He said: "The cerebral ganglia are large . . . and are united by a very broad commissure, and with the pleural and pedal ganglia form a well-marked circum-œsophageal ring." He mentioned a "pleuro-visceral mass," giving rise to many nerves, but gave no exact account of the number or distribution of those nerves.

The nervous system of *Acavus* is closely covered with connective tissue, which is very difficult to dissect away, even in fresh material. The cerebro-pleural and cerebro-pedal connectives are closely bound together. The pedal ganglia are completely fused. On the ventral surface of the visceral chain three divisions can be distinguished, but dorsally it appears to be a solid mass. The visceral nerves are similar to those of *Borus*.

7. Onchidium type.

Under this heading are included members of the Basommatophoran families Ancyliidæ and Siphonariidæ, and of the Stylommatophoran family Onchidiidæ.

STYLOMMATOPHORA.

i. ONCHIDIIDÆ.

E. g., *Onchidella capensis* (Pl. 5. fig. 61).—This nervous system has already been described on p. 17.

According to Plate (1891) the nervous system of *Onchidium peroni* (Pl. 5. fig. 62) is of this type, although it is less concentrated, the commissures and connectives being longer. Eight visceral nerves are figured—two from the abdominal ganglion; one to rectum, mantle, and kidney; two to aorta, mantle, and genitalia; and three from each pleuro-parietal ganglion to body-wall and mantle.

BASOMMATOPHORA.

i. ANCYLIDÆ.

E. g., *Ancylus lacustris* (Pl. 1. fig. 11). (*André*, 1893.)—The cerebral ganglia are large, and are joined by a commissure of moderate length. The cerebro-pedal connectives are very short. The left cerebro-pleural connective is only half as long as the right one. The pleural and parietal ganglia are fused together, the abdominal ganglion being more widely separated from them on the right than on the left. André did not name the visceral ganglia, but figured nerves arising from all three, so that it seems likely that fusion has taken place, according to this type.

According to Moquin-Tandon (1885), *Ancylus fluviatilis* also has three visceral ganglia, but he gives no description, and the figure is unlabelled.

ii. SIPHONARIIDÆ.

E. g., *Siphonaria pectinata*. (*Köhler*, 1894.)—The cerebral ganglia are united by a fairly long commissure. The cerebro-pleural and cerebro-pedal connectives are short. The pedal ganglia are united by two commissures; the pleuro-pedal connectives are short. There are three ganglia in the visceral chain, two "pleuro-intestinal" or pleuro-parietal ganglia, and an abdominal ganglion. They are united by short lengths of commissure. The right pleuro-parietal ganglion gives off three large nerves: (1) to the osphradium; (2) to the mantle; (3) to the anterior region of the mantle. The abdominal ganglion gives off three nerves: (1) to pericardium and kidney; (2) to the genitalia; (3) to the rectum, body-wall, and mantle-edge. The left pleuro-parietal ganglion gives rise to two nerves: (1) to the body-wall; (2) Köhler could not trace this nerve.

8. Vaginula type.

Under this heading are included members of the Stylommatophoran families Helicidæ, Achatinidæ, Philomycidæ, Vaginulidæ, Janellidæ

i. VAGINULIDÆ.

E. g., *Meisenheimeria alte*. (Hoffmann, 1925).—This nervous system has been described on p. 17.

According to Hoffinan, *Sarasimula plebeja* has a nervous system resembling that of *Meisenheimeria*, as has also *Vaginula* (Simroth, 1910).

ii. JANELLIDÆ.

The visceral ganglia are fused into a solid mass in the nervous systems of this family, according to Simroth (1910), but Plato (1898) distinguishes three indistinct divisions in *Janella schauinslandi* and *Aneitella berghi*.

iii. PHILOMYCIDÆ.

E. g., *Philomyrus bilineatus* (Pl. 4. fig. 59). (Hoffmann, 1924).—The whole nervous system is very much concentrated and the visceral chain shows five indistinct parts.

iv. HELICIDÆ.

E. g., *Helicostyla najas*.—The cerebral ganglia have three lobes, which can be distinguished when the connective tissue has been dissected off, and which are joined by a short commissure. The cerebro-pleural and cerebro-pedal connectives are of moderate length, and are closely bound together by the connective-tissue sheath. It is not possible to dissect the components of the visceral chain, or to separate them from the pedal ganglia, or to distinguish between pleural and pedal nerves, as the connective-tissue sheaths adhere so tightly to them.

v. ACHATINIDÆ.

E. g., *Cochlitoma zebra*.—Robson (1921) described and compared the nervous systems of two varieties of *Cochlitoma zebra*, vars. *obesa* and *fulgurata*. The cerebral ganglia are joined by a stout commissure. The several elements of the visceral commissure are very closely united, and on the right side no distinction between the abdominal and parietal and pleural ganglia could be made out. On the left side the pleural and parietal ganglia could just be distinguished, but the division between the parietal and abdominal

ganglion was less clear. Close approximation between the pedal and visceral masses is characteristic of this nervous system, the pedal ganglia being completely fused. A dense coat of connective tissue encases the whole nervous system, so that even the roots of the nerves are difficult to distinguish.

VIII. DISCUSSION AND SUMMARY.

One of the objects of this research was to discover whether there was any correlation between the modifications of the nervous system and the indications of affinity based on other organs. Using Pilsbry's classification of the Pulmonata (see pp. 23-24), and his suggestions as to family and generic relationships, it is possible to find out, in cases where the affinities have been worked out in detail, whether the lines of modification of the nervous system follow those of general morphology.

It should be pointed out that Pilsbry's classification is the only comprehensive one up to date, although several authors (Watson, Hoffman, etc.) have examined groups of families intensively. It very largely depends on the characters of single systems—thus the primary subdivisions of the Vasopulmonata are based on the characters of the ureter. Without committing myself to any statement as to what an ideal classification of the Pulmonata should be, I wish to point out that the present research has brought to light various cases in which the evidence as to systematic position based on one set of organs contradicts that based on another.

I have arranged the eight types of nervous system with the families and genera belonging to each type in tabular form (see Table I, p. 48). It will be seen that some families have a very constant type of nervous system, whereas in others there is a considerable degree of variation.

The Basommatophora, which are regarded as being primitive Pulmonates, will be seen to possess unspecialized nervous systems of the first type—a few forms exhibiting more concentration, and therefore being included under Type II, and one form under Type VII.

Those families which are regarded by systematists as being derived independently of the main lines of Pulmonate evolution have concentrated types of nervous system, *e. g.*, Onchidiidæ (Type VII), Janellidæ (Type VIII), Vaginulidæ (Type VIII).

The families belonging to the Vasopulmonate subgroups Agnathomorpha and Aulacopoda, *i. e.*, the Slugs, and the Agnatha, *i. e.*, the carnivorous Snails, do not show much variation in the type of nervous system. It is in the Holopoda where the greatest variation occurs, a subgroup which was regarded by Pilsbry as containing "numerous family groups of very unequal relationships *inter se*." In Pilsbry's (1894) classification of the family

TABLE I.

TYPE I.	TYPE II.	TYPE III.	TYPE IV.	TYPE V.	TYPE VI.	TYPE VII.	TYPE VIII.
<p>BASOMMATOPHORA.</p> <p>(i) Amphibolidæ. e. g., <i>Amphibola</i>.</p> <p>(ii) Ellobiidæ. e. g., <i>Auricula</i>, <i>Carychiwm</i>, <i>Marinula</i>.</p> <p>(iii) Limnæidæ. e. g., <i>Limnæa</i>, <i>Amphi-</i> <i>peplea</i>.</p> <p>(iv) Otinidæ. e. g., <i>Otina</i>.</p>	<p>BASOMMATOPHORA.</p> <p>(i) Ancyliidæ. ← e. g., <i>Ancylus</i> <i>capuloides</i>.</p> <p>(ii) Physidæ. e. g., <i>Physa</i>.</p> <p>(iii) Planorbidæ. e. g., <i>Planorbis</i>, <i>Isidora</i>.</p>					<p>BASOMMATOPHORA.</p> <p>(i) Ancyliidæ. e. g., <i>Ancylus</i> <i>lacustris</i>.</p> <p>(ii) Siphonariidæ. e. g., <i>Siphonaria</i>.</p>	

TABLE I (cont.).

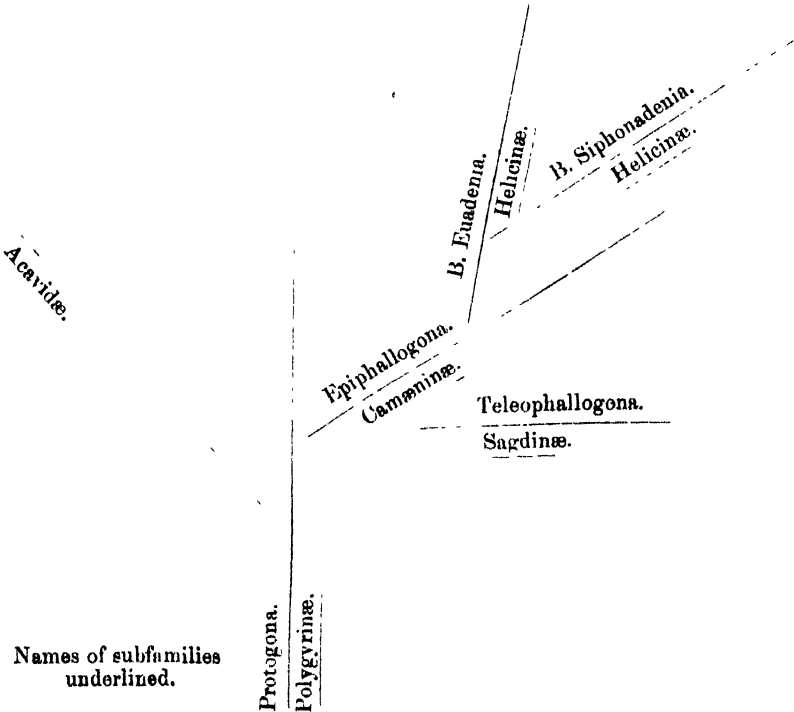
TYPE I.	TYPE II.	TYPE III.	TYPE IV.	TYPE V.	TYPE VI.	TYPE VII.	TYPE VIII.
	(ii) Helicidæ. e.g., <i>Amphidromus</i> , <i>Camena</i> , <i>Euparypha</i> , <i>Hadra</i> , <i>Oreohelix</i> , <i>Solaropsis</i> .	→	(i) Helicidæ. e.g., <i>Ashmolella</i> , <i>Albersia</i> , <i>Euhadra</i> , <i>Helix</i> , <i>Helicella</i> , <i>Papuna</i> , <i>Planispira</i> , <i>Polygyra</i> , <i>Sonorella</i> , <i>Theba</i> .	(i) Helicidæ. e.g., <i>Hygromia</i> , <i>Ochthe- phila</i> .		→	(ii) Helicidæ. e.g., <i>Helicostyla</i> .
	(iii) Urocoptidæ. e.g., <i>Brachypodella</i> .	→	(ii) Urocoptidæ. e.g., <i>Berendia</i> , <i>Euca-</i> <i>lodium</i> .				
	(iv) Eulotidæ. e.g., <i>Eulota</i> .	→					
	(v) Bulimulidæ. e.g., <i>Orhatenus</i> , <i>Oxystyla</i> .	→	(iii) Bulimulidæ. e.g., <i>Bulinulus</i> , <i>Placo-</i> <i>sphus</i> .				
	(vi) Cerionidæ. e.g., <i>Cerion</i> .				(i) Acavidæ. e.g., <i>Acanus</i> , <i>Ampelita</i> , <i>Bornis</i> , <i>Helico-</i> <i>phanta</i> .		
		(ii) Endodontidæ. e.g., <i>Goni-</i> <i>discus</i> , <i>Patula</i> .					

Helicidæ the fact has already been referred to (p. 2) that he did not take the structure of the nervous system into consideration. He classifies the Helicidæ as follows:—

SUBDIVISION.	SUBFAMILY.	GENERA.
1. Protogona.	Polygyrinæ.	<i>Polygyra</i> , <u><i>Ashmunella</i></u> , <u><i>Solaropsis</i></u> , <u><i>Praticolella</i></u> , etc.
2. Teleophallo'gona.	Sagdinæ.	<i>Sagda</i> , <i>Thysanomorpha</i> , <i>Zaphysema</i> .
3. Epiphallo'gona.	Camæninæ.	<i>Camæna</i> , <i>Euhadra</i> , <u><i>Amphidromus</i></u> , <u><i>Planispira</i></u> , <u><i>Albersia</i></u> , <u><i>Papuina</i></u> , etc.
4. Belogona, Euadenia.	Helicinæ.	<u><i>Oreohelix</i></u> , <u><i>Sonorella</i></u> , <u><i>Helicostyla</i></u> , <u><i>Leucochroa</i></u> , etc.
5. Belogona, Siphonadenia.	Helicinæ.	<u><i>Helicella</i></u> , <u><i>Helix</i></u> , <u><i>Ochthephila</i></u> , <u><i>Hygromia</i></u> , <u><i>Theba</i></u> , <u><i>Leptaxis</i></u> , etc.

(Those genera about whose nervous systems I have been able to obtain information are underlined.)

TABLE II.

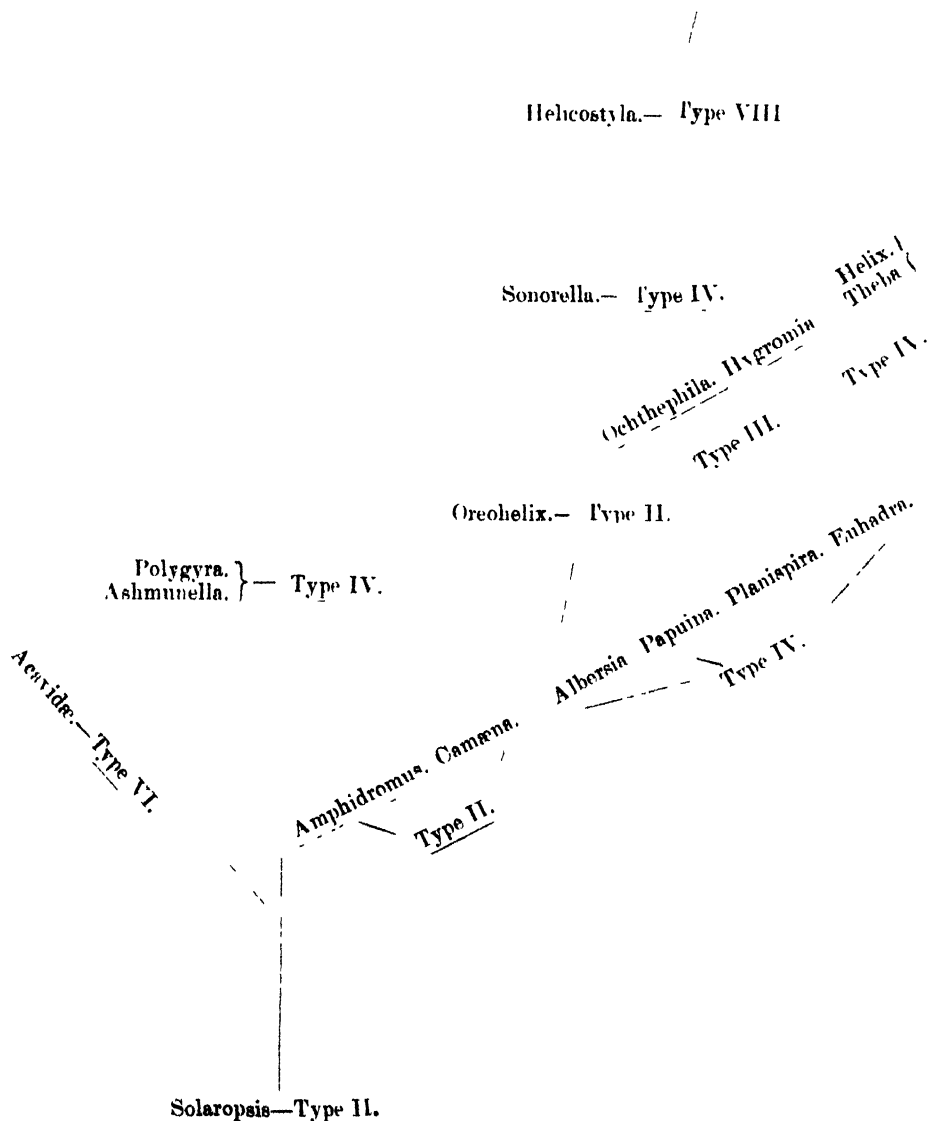


The *Protogona* Pilsbry regarded as being near the ancestral stock of the *Helicidæ*, from which arose the *Teleophallologona* and the *Epiphallologona*, the latter giving rise to the *Belogona euadenia*, from which originate the *Belogona siphonadenia*.

Diagrammatically the lines of relationship appear somewhat as in Table II (see p. 52), the families belonging to Pilsbry's subdivisions being included.

Substituting, in place of the sub-divisions and families, the genera and their types of nervous system, the following table is obtained :—

TABLE III.



This seems to suggest that there is a residual line of unspecialized forms in the Helicidæ off which the more complex forms of nervous system have been developed. The variation in the structure of the kidney has had an analogous history. In *Solaropsis* the ureter is straight and opens on a papilla fairly far forward in the mantle-cavity. *Amphidromus* also has this primitive type of kidney. *Papuina*, on the other hand, has a long reflexed ureter, and so have *Helicostyla*, *Helix*, and *Hygromia*, whereas *Ochthephila* and *Theba* have short reflexed ureters, the excretion being carried out of the mantle-cavity by an anterior groove. I have not been able to find descriptions of the kidney of the other genera.

In treating forms with Type IV nervous system as actually springing from more primitive forms having a nervous system of Type II, I am accepting Pilsbry's provisional phylogenetic scheme, though it is likely that further subdivision of the Helicidæ is necessary, or that some of the genera should be included elsewhere. On the whole, the inter-relationships of these genera, as suggested by Pilsbry, and the apparent evolution of more concentrated forms of nervous system from less concentrated ones are correlated; but anomalies are to be found of such an order as to suggest that the position of a family or a genus determined by considerations of a single system is very much open to question. Thus from evidence of the nervous system alone the Aperidæ (subgroup Agnathomorpha) would be closely allied to the Helicidæ (Holopoda), both possessing an Heliciform type of nervous system. Watson (1920) has also shown the confusion which can arise by considering relationships based on single characters. In short, we are at present only in the position of being able to speak concerning the evolution of the nervous system, genitalia, and ureter separately. What we do not know is how far the evolution of these and other organs can be synthesized in individual cases.

In addition, it should be pointed out that there may be very abrupt evolutionary changes. Pilsbry (1894) regarded the Acavidæ (see Tables II and III) as derived from the unspecialized *Protogona*. The Acavidæ have a uniform type of nervous system, showing a fairly advanced stage of concentration Type VI, and no intermediate stages from Type II of the *Protogona* are met with. If Pilsbry is correct in his suggestions as to these inter-relationships, either there may have occurred great extinction of intermediate forms, or else this is an example of a large mutant.

On the other hand, the evidence afforded by modifications of the nervous system is in accord with Pilsbry's (1906) views as to the phylogeny of the Achatinidæ. They are supposed to be derived from an ancestral Clausilian stock, the subfamily Stenogyrinæ being less specialized than the Achatininæ. The nervous system of *Clausilia* (see Table I, p. 48) belongs to Type I; that of *Stenogyra* and *Pseudoglossula* (Stenogyrinæ) to Type II;

that of *Subuliniscus* (Stenogyrinæ) to Type II; that of *Burtoa* and *Achatina* (Achatininæ) to Type II; and that of *Cochlitoma* (Achatininæ) to Type VIII.

From Table I it will be seen that among most of the other Pulmonate families the type of nervous system remains very constant. It is possible that, where the type is the same, small differences as to length of commissures may occur in the families, but in most instances there is not enough evidence on this point. Hoffmann (1924, 1925) does not mention any striking specific differences in his monographs on the Philomycidæ and Vaginulidæ. Watson (1915) examined a number of different species of *Apera*, and noted differences in the length of the connectives and commissures and the quantity of connective tissue wrapping over the ganglia, but the arrangement of the visceral ganglia remains constant.

In the Basommatophoran family Ancyliidæ, a different type of nervous system is met with in *Ancylus capuloides* (Type II) and *Ancylus lacustris* (Type VII), and again in the Rhytididæ, *Rhytida capillacea* comes under Type II and *R. inæqualis* under Type IV.

In conclusion, the results of this research may be summed up as follows:—

1. The visceral ganglia in the Pulmonata exhibit a tendency to become concentrated in the course of their evolution.

2. In course of condensation the identity of the visceral ganglia is often confused, and can only be determined by a knowledge of the distribution of the visceral nerves.

3. There are eight types into which the Pulmonate nervous system can be divided according to the degree and mode of concentration of the visceral ganglia.

4. These types are fairly sharply defined, but there are instances in which it is difficult to decide the type to which the nervous system belongs.

- 4a. Variation in the type of nervous system takes place within families and within genera.

- 4b. Slight variation takes place within species, but not enough to affect the combination of the ganglia as a whole.

5. Systematic position should, of course, not be decided by consideration of one character alone, but consideration of the nervous system affords valuable evidence as to the relationships of families to one another and genera within families.

6. Comparison of the grouping of the nervous system under the eight types with groupings based on systematic classification reveal in some cases very clearly that affinities are by no means well understood, and that our present method of indicating affinity by the systematic treatment of single-organ systems may involve very serious contradictions and anomalies.

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EXPLANATION OF THE PLATES.

PLATE 1.

- Fig. 1. *Chilina dombeina*. (After Plate.)
 2. *Chilina mulleri*. (After Pelseneer.)
 3. *Latia neritoides*. (After Pelseneer.)
 4. *Auricula myosotis*. (After Pelseneer.)
 5. *Amphibola murexavellana*. (After Pelseneer.)
 6. *Carychium minimum*. (After Simroth.)
 7. *Marinula juanensis*. (After Odhner.)
 8. *Physa acuta*. (After Lacaze-Duthiers.)
 9. *Lamnæa stagnalia*. (After Lacaze-Duthiers.)
 10. *Isidora globosa*. (After Connolly & Watson.)
 11. *Ancylus lacustris*. (After André.)
 12. *Ancylus fluviatilis*. (After Moquin-Tandon.)
 13. *Vallonia costata*. (After Watson.)
 14. *Putulastra balmei*. (After Watson.)
 15. *Colulinus junodi*. (After Connolly & Watson.)

PLATE 2.

- Fig. 16. *Cochlicopa lubrica*. (After Simroth.)
 17. *Patula rotundata*. (After Simroth.)
 18. *Solaropsis* sp.
 19. *Cumæna senegalensis*.
 20. *Amphidromus atricallosus*.
 21. *Ashmunella cockerelli*.
 22. *Polygyra albolabris*.
 23. *Planispira surrecta*. (After Simroth.)
 24. *Papuina moseleyi*.
 25. *Helix pomatia*.
 26. *Oreohelix cooperi*.
 27. *Eulota similis*.
 28. *Ochthephila terricola*. (After Watson.)
 29. *Helicella scetzeni*.
 30. *Theba rot*.

PLATE 3.

- Fig. 31. *Hygromia limbata*. (After Watson.)
 32. *Helicophanta sowerbyana*.
 33. *Ampelita xystera*.
 34. *Borus* sp. (showing the pigmented area—stippled).
 35. *Bulinulus interruptus*.
 36. *Bulinulus interruptus* (pedal and visceral mass only)
 37. *Orthalicus zebra*.
 38. *Oxystyla bensoni*.
 39. *Euparypha pisana*.
 40. *Placostylus bivaricosus*.
 41. *Cerion* sp.
 42. *Brachypodella agnesiana*. (After Pilsbry.)
 43. *Brachypodella* (*Cyhdrella*) *bruccidi*.
 44. *Eucalodium ghiesbreghti*. (After Fischer & Crosse.)

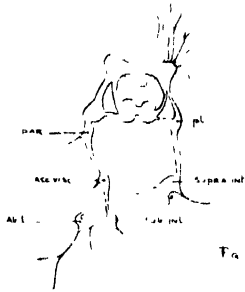


Fig. 1

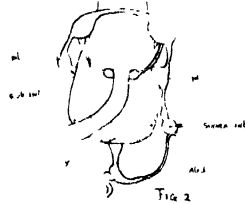


Fig. 2

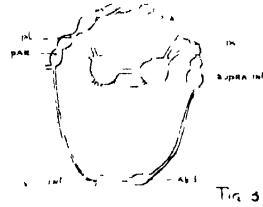


Fig. 3



Fig. 4

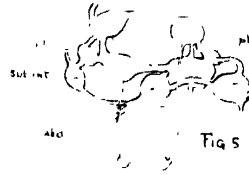


Fig. 5

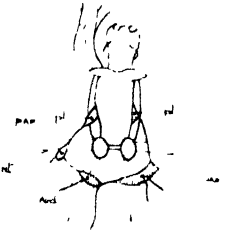


Fig. 6

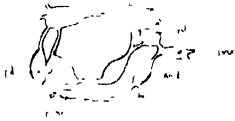


Fig. 7

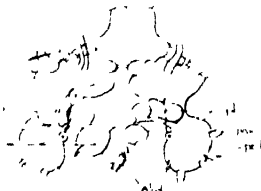


Fig. 8

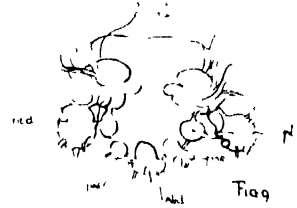


Fig. 9

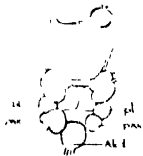


Fig. 10

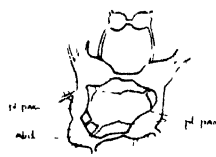


Fig. 11



Fig. 12

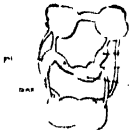


Fig. 13

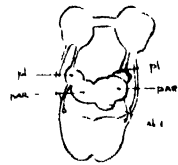


Fig. 14

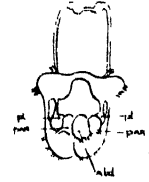


Fig. 15

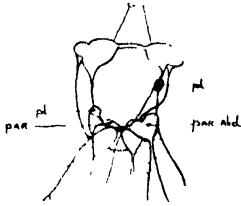


Fig 16

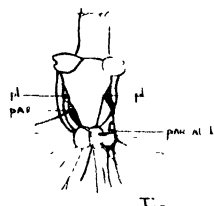


Fig 17

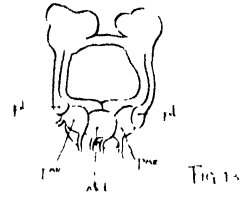


Fig 18

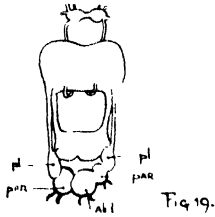


Fig 19.

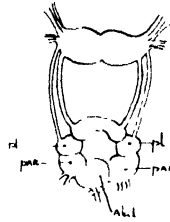


Fig 20

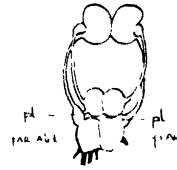


Fig 21



Fig 22

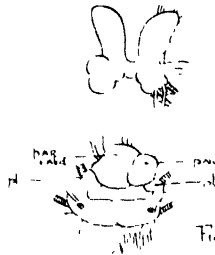


Fig 23



Fig 24

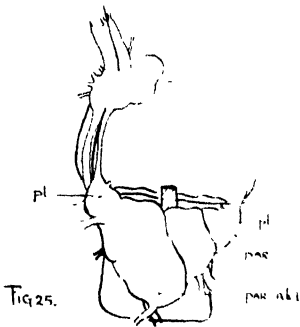


Fig 25.



Fig 26



Fig 27

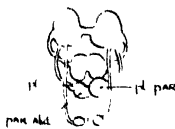


Fig 28



Fig 29



Fig 30

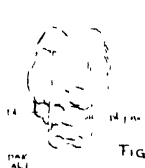


FIG. 31



FIG. 32



FIG. 33

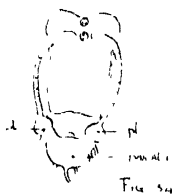


FIG. 34



FIG. 35

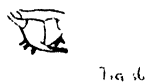


FIG. 36

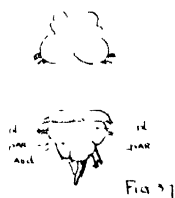


FIG. 37

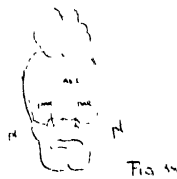


FIG. 38

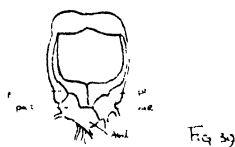


FIG. 39



FIG. 40

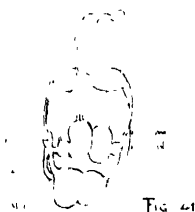


FIG. 41



FIG. 42



FIG. 43



FIG. 44

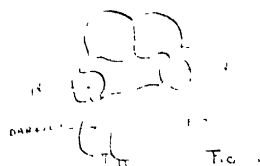


FIG. 45



Fig. 45

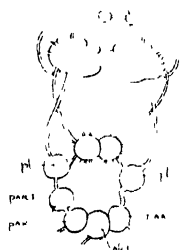


Fig. 47

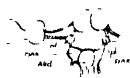


Fig. 46

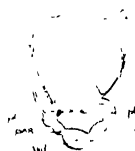


Fig. 49



Fig. 50



Fig. 51



Fig. 52



Fig. 53



Fig. 54



Fig. 55



Fig. 56



Fig. 57



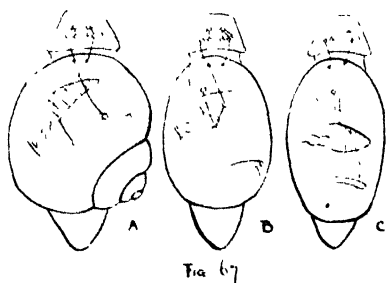
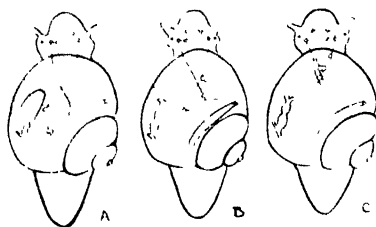
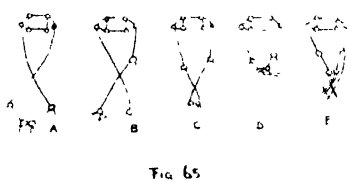
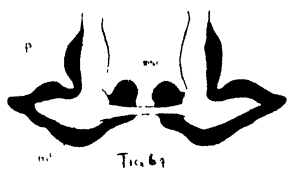
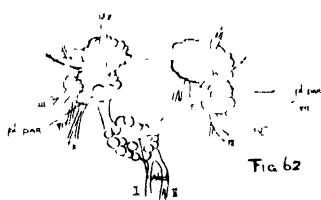
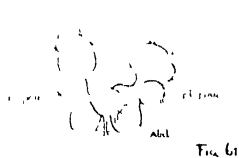
Fig. 58



Fig. 59



Fig. 60



CENTRAL NERVOUS SYSTEM IN THE GASTROPODA PULMONATA.

PLATE 4.

- Fig. 45. *Berendtia taylori*. (After Fischer & Crosse.)
 46. *Balea perversa*. (After Simroth.)
 47. *Stenogyra decollata*. (After v. Jhering.)
 48. *Stenogyra decollata*.
 49. *Pseudoglossula cressyi*. (After Connolly & Watson.)
 50. *Subuliniscus chiradzulensis*. (After Connolly & Watson.)
 51. *Achatina fulica*.
 52. *Burtoa arnoldi*.
 53. *Ennea dussmieri*. (After Weigmann.)
 54. *Testacella fischeriana*. (After Plate.)
 55. *Daudebardia rufa*. (After Plate.)
 56. *Zonites cellarius*. (After Lacaze-Duthiers.)
 57. *Helicarion gomesianus*. (After Watson.)
 58. *Ledoulxix mozambicensis*. (After Connolly & Watson.)
 59. *Philomycus bilineatus*. (After Hoffmann.)
 60. *Omalonyx ungius*. (After Pelseneer.)

PLATE 5.

- Fig. 61. *Onchidella capensis*. (After Watson.)
 62. *Onchidium peroni*. (After Plate.)
 63. *Helix pomatia*: cerebral ganglia, showing nerves. (After Bang.)
 64. *Helix pomatia*: longitudinal section through cerebral ganglia, showing distribution of nerve-cells and fibres. (Nerve-cells = black band.) (After Moisenheimer.)
 65. Diagram to show transition from the chistoneurous to the euthyneurous condition. A = Prosobranch; B = *Chilina*; C-E = diagrammatic. (After Merker.)
 66. Diagram to show transition from the chistoneurous to the euthyneurous condition. A = Prosobranch; B = *Chilina*; C = Basom. (After Naef.)
 67. Diagram to show detorsion in Opisthobranchs. A = Actæonidæ; B = *Actæon*; C = *Bulla*.

CONTRACTIONS.

- | | |
|--------------------------------|------------------------------|
| 1 = olfactory nerve. | 6 = med. labial nerve. |
| 2 = optic nerve. | 7 = ext. " " |
| 3 = ext. peritentacular nerve. | 8 = cerebral arterial nerve. |
| 4 = int. " " | 9 = auditory nerve. |
| 5 = int. labial nerve. | |
-
- | | |
|--|--|
| <i>pc.</i> = procerebrum. | <i>par.</i> = parietal ganglion. |
| <i>mc.</i> = mesocerebrum. | <i>ped.</i> = pedal ganglion. |
| <i>mtc.</i> = metacerebrum. | <i>pl.</i> = pleural ganglion. |
| <i>acc. visc.</i> = accessory visceral ganglion. | <i>sub-int.</i> = sub-intestinal ganglion. |
| <i>abd.</i> = abdominal ganglion. | <i>supra-int.</i> = supra-intestinal ganglion. |
-

New and interesting Species of *Scalpellum* from a Telegraph Cable near the Coast of North Chile. By C. A. NILSSON-CANTELL, Fil.Dr. Sweden.
(Communicated by Dr. W. T. CALMAN, F.R.S., F.L.S.)

(With 6 Text-figures.)

[Read 15th November, 1928.]

INTRODUCTION.

The west coast of North and South America was, as regards the Cirripedes, regarded as one province (numbered respectively 2 and 8) by Darwin (1851) and Hook (1883). Darwin had, however, thought of dividing it into subprovinces—north and south of the equatorial region. Ortmann (1896) divided the region into three parts for littoral and pelagic animals in this ocean.

Since Darwin several authors, *e. g.*, Wettner, Pilsbry, Broch, Cornwall, and the author have noted localities for the Cirripedes from the waters of the west American coast—most of these being from the North American part.

The cold Peru stream of the South American coast affords with regard to temperature the same conditions for the littoral animals as in the boreal region by the North American coast. Not many Cirripedes are found to be distributed along the whole American west coast, which may be due to our very insufficient knowledge. As eurytherm species (also taken from the littoral of the equatorial region) the following may be mentioned :—*Pollicipes elegans*, *Balanus tintinnabulum*, *B. concavus*, *B. trigonus*, *B. levis*, *Tetracrita porosa*. The two last-mentioned *Balanus* species have a wider distribution, as they are also found from the east coast of South America. It may be pointed out that the species of the genera *Balanus* and *Tetracrita* above quoted have split into many local races or subspecies.

The material here determined is taken from the west coast of South America, near the north coast of Chile, from deep waters (343–400 fathoms). Most Cirripedes noted from this coast belong to the littoral fauna and especially to the genera *Pollicipes*, *Verruca*, *Balanus*, *Elminius*, and *Tetracrita*. Of cosmopolitan pelagic forms the genera *Lepas*, *Conchoderma*, *Coronula*, *Tubicinella*, *Chelonibia*, and *Platylepas* may be mentioned from these South American waters, but many may be added in the future.

We do not know much about the animals living in deep waters from this part of the ocean. As regards the only genus represented in this material, *Scalpellum*, which with some exceptions lives in deep waters, I find in the

literature the following species from the Galapagos Islands and the coast from Chile down to Cape Horn :

Species.	Locality.	Depth in Fathoms.
<i>Scalpellum salartiae</i> Gruvel, 1901	Cape Horn.	481
„ <i>gibberum</i> Aurivillius, 1894	Magellan Strait.	10-29.5
„ <i>recurvirostrum</i> Hoek, 1883	South Chile.	141
„ <i>minutum</i> Hoek, 1883.....	South Chile.	1475
„ <i>darwini</i> Hoek, 1883	Middle Chile.	2147
„ <i>chiliense</i> Pilsbry (1907), 1908*..	Middle Chile.	677
„ <i>soror</i> Pilsbry, 1907.....	Galapagos Islands.	634
„ <i>galapaganum</i> Pilsbry, 1907	Galapagos Islands.	634

Of these *S. gibberum* is to be noted also from the Atlantic coast of South America. To this list, I believe, much will be added.

The material now described was collected from a telegraph-cable by the Eastern and Associated Telegraph Companies' cable-ship 'Retriever,' and contains four species of *Scalpellum*—two of them, *S. projectum* and *S. retrieveri*, being new to science, while, of the other two, *S. soror*, described by Pilsbry (1907 *a*) from the Galapagos Islands, is here for the first time re-identified from neighbouring waters. The fourth species, *S. gruvelianum*, also first described by Pilsbry (1907 *b*) from the Californian coast but later on re-identified by Broch (1922) from British Columbia, is now to be noted from South American waters also. (For the distribution of *S. gruvelianum*, see page 74.)

DESCRIPTIONS.

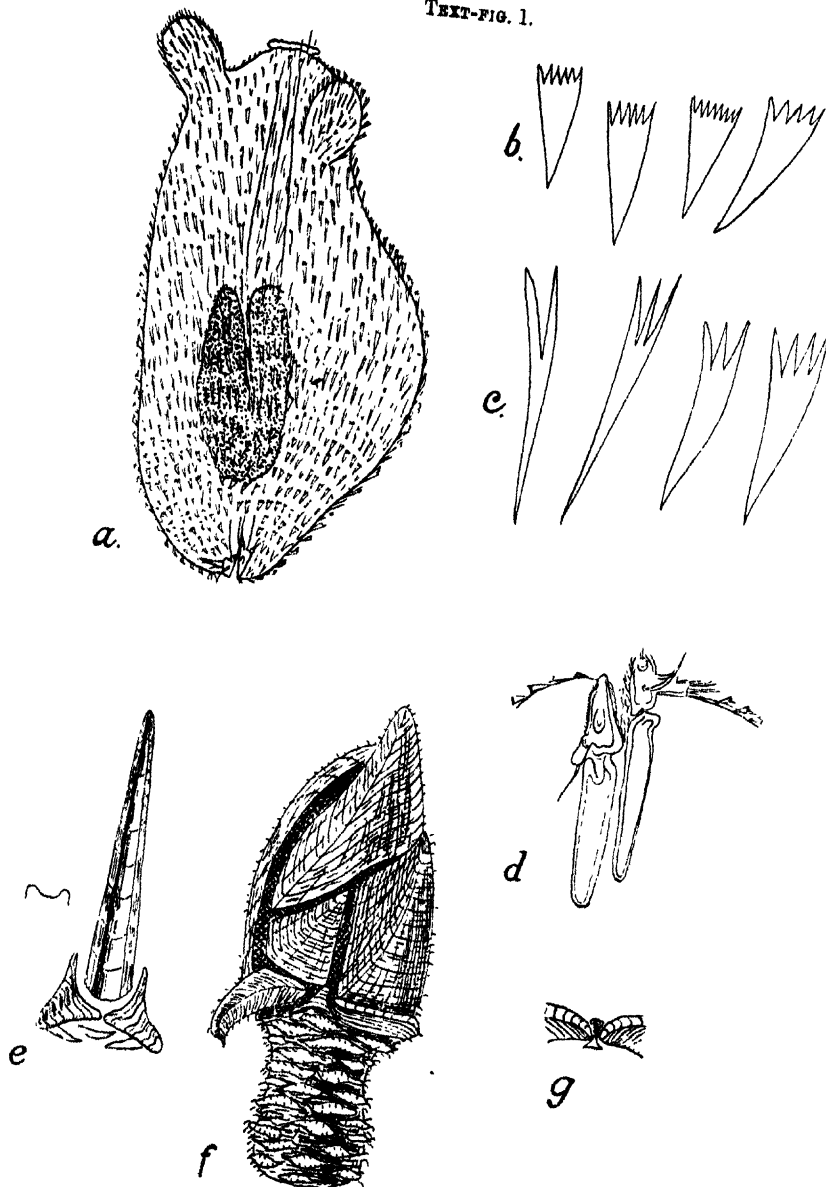
SCALPELLUM PROJECTUM, sp. n. (Text—figs. 1, 2.)

Holotype: in the British Museum (Natural History), London.

Diagnosis. Female: capitulum with 14 plates separated by distinct chitinous interspaces; a thick hairy cuticle; growth-lines and radial striae well marked. Scutum quadrangular; ocludent margin convex. Carina long, regularly arched; umbo apical; the roof concave with bordering ribs. Upper latus quadrangular; umbo apical. Rostrum small, covered by the latera. Rostral latus very low. Inframedian latus broadly triangular; the umbo at the apex.

* This species was first described under the name *S. gracile* (1907 *a*) by Pilsbry. Pilsbry, who (1908) stated the name *gracile* to be a homonym, gave the species a new name, *chiliense*. This was not noticed by Gruvel, who (1920) proposed the name *neogracile*.

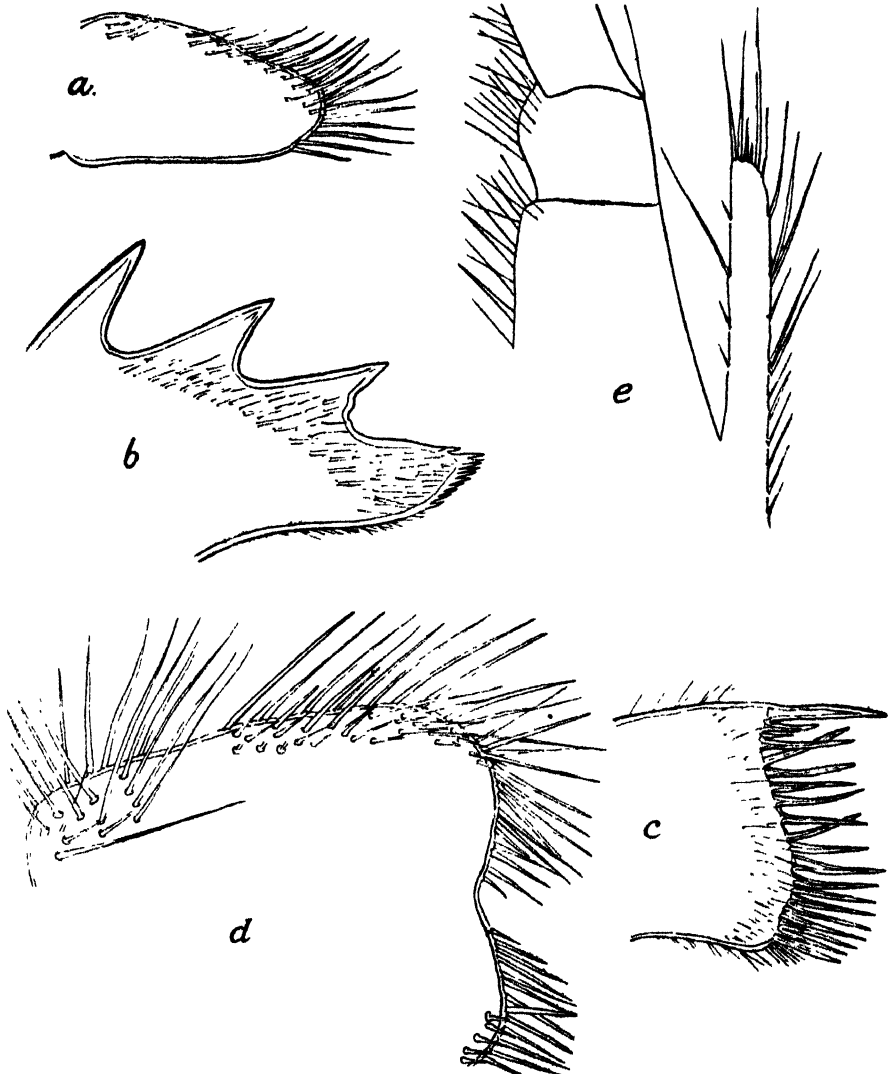
TEXT-FIG. 1.



Scalpellum projectum Nilsson-Cantell, sp. n.
 a. Complemental male. b, c. Spines from the surface of the male. d. Prehensile antennæ of the male. e. Carina and carinal latera. f. The animal, lateral view. g. Rostrum and rostral latera.

Carinal latus with projecting umbo; the carinal side concave. Peduncle shorter than the capitulum with transversely elongated scales. Mandible with three teeth and a pectinated inner angle. Maxilla I. with sinuous edge

TEXT-FIG. 2.



Scalpellum projectum Nilsson-Cantell, sp. n.

a. Palpus. b. Mandible. c. Maxilla I. d. Maxilla II.

e. Cirrus VI. and caudal appendage.

without a notch. Maxilla II. with bristles in three groups. Complemental male sack-like without plates and cirri; some lobes round the opening; surface with divided spines.

Description. The collection contained one very large *Scalpellum* individual belonging to the group of *Scalpellum arietinum* Pilsbry (1907 a) with very characteristic projecting carinal latera. The two species described by Pilsbry (1907 a) from the Gulf of Mexico, *S. arietinum* and *S. diceratum*, are both smaller; judging from external characters (internal parts are unfortunately not described) this specimen comes nearer to the latter species. One possibility is that they all belong to the same species but represent different ages. Yet the differences in the external characters, as, e. g., the carina, are so great that this individual must be regarded here as a new species.

Capitulum was covered with a thick hairy cuticle, after removing which the shape of the plates could be studied. The 14 plates were well calcified with growth-lines and fine radial striæ well developed; they are distinctly separated by chitinous interspaces, especially wide between the carina and neighbouring plates.

Scutum quadrangular with the ocludent margin convex. Umbo is terminal with a distinct diagonal ridge to the opposite angle. The tergal margin is hollowed out, the lateral and basal margins straight.

Tergum large, triangular; with ocludent margin convex, basal and carinal margins sinuous. There is a distinct diagonal ridge from the apex.

Carina long, regularly arched, with an apical umbo. The roof, in contrast to Pilsbry's two species, is concave with well-marked bordering ribs. As regards the apical umbo there is some resemblance to *S. diceratum*, but a difference in the concave dorsal roof.

Upper latus is quadrangular, the scutal and tergal margins equal in length. The basal margin is a little shorter, and the carinal margin is about half of the basal margin. All margins are nearly straight; umbo apical. This plate differs from the corresponding plate in the species mentioned.

Rostrum small, in the upper part covered by the carinal latera. The lower part is free and triangular.

Rostral latus low, being curved near the umbo, from which two parallel ridges run to the carinal end.

Inframedian latus, broadly triangular, has an apical umbo curved towards the rostrum. This plate is most like that of *S. diceratum*, but is broader.

Carinal latus is very peculiar in shape, as the umbo projects behind and at the sides. The distance between the umbones of the two latera is 21 mm. A distinct ridge goes from the umbo to the angle between the upper and lateral margin of the plate. The dorsal side is distinctly concave. In a dorsal view it is seen that the carina extends down to half of the carinal latera, and thus not so far down as in Pilsbry's species. The latera are most like those of *S. arietinum*, which differs considerably in the other plates.

Peduncle about half of the capitulum, with closely-placed, large, transversely-elongated scales. There are small bristles over the whole surface, as on the capitulum.

Mouth-parts. *Labrum* armed with teeth.

Palpus conical, but blunt with bristles at the edge and the point.

Mandible with three teeth and a pectinated inner angle.

Maxilla I. with a straight, somewhat sinuous edge, without a notch.

Maxilla II. with a spineless slight notch on the middle of the front edge.

A posterior lobe is indistinctly differentiated.

Measurements (in millimetres) :—

Length of capitulum, 50.

Breadth of capitulum, 32.

Length of peduncle, 26.

Breadth of peduncle, 20.

Number of segments * of the Cirri :—

I.	II.	III.	IV.	V.	VI.	Caudal appendage.
<u>11</u> <u>19</u>	<u>26</u> <u>26</u>	<u>30</u> <u>31</u>	<u>32</u> <u>33</u>	<u>31</u> <u>32</u>	<u>29</u> <u>33</u>	1

Cirrus I. with unequal rami, the shorter ramus with much expanded segments, as, for instance, in *S. velutinum*. The other cirri with nearly equal rami. The caudal appendage somewhat longer than the proximal segment of the protopodite. Bristles at the top and the side.

No penis.

Complemental males were met with at the inside of the scuta near the apex; three on the right and one on the left side. The male was of the sack-like type without any traces of plates. On the largest male (length 2.20 mm.) there are two small lobes at the pole, where the opening for the genital organs is situated; in younger specimens these processes are wanting: the male can thus have a very varying form. The male here figured comes nearest to that figured for *S. eximium* (syn. to *S. velutinum*) by Hoek (1883, pl. ix, fig. 10). For *S. velutinum* younger males are figured also without these processes. At the opposite pole of the male two prehensile antennæ are situated; the detailed form of these could not wholly be made out (text-fig. 1, *d*), but I think there are not many differences in this regard between the *Scalpellum* species. Of internal organs only the testis with a vas deferens can be distinguished. Over the surface there are relatively large spines divided at the top; some enlarged spines are figured from the anterior (text-fig. 1, *b*) and from the posterior part of the body (text-fig. 1, *c*). It is noteworthy that Hoek in *S. eximium* figures nearly similar spines.

Locality. Lat. 19° 26' S., long. 70° 27' W. (343–400 fathoms; C.S. 'Retriever'). Presented by Eastern and Associated Telegraph Companies.

Affinities. This species belongs to the group of *S. arietinum* Pilsbry (1907 *a*), characterized by the projecting carinal latera, but may be distinguished in external characters from both previously known species, for which

* Numbers of segments refer to the individuals for which measurements are given.

descriptions of internal parts are wanting. In the mouth-parts and the reduced complemental male some relations exist with *S. velutinum* and its allies, which, however, in external characters are well distinguished.

SCALPELLUM SOROR Pilsbry, 1907. (Text-fig. 3.)

Scalpellum soror Pilsbry (1907 a).

Complementary Description.

Of this species, only once before described by Pilsbry from the Galapagos Islands, one wholly-developed specimen was re-identified together with *S. gruvelianum* Pilsbry, 1907 b. At first I thought these might belong to the same species, as internal parts are very like and also resemblances in external characters exist, but a close study of the material proved that these are good species, *S. soror* differing in the form of the capitulum and the very typical inframedian latus. For comparison a figure of the animal is given (text-fig. 3), showing total agreement with that of Pilsbry. To the description given by Pilsbry for the external parts nothing needs adding. As the internal parts were wholly unknown, they may be here described.

Mouth-parts. *Labrum* with teeth.

Palpus conical, with bristles at the point and the upper edge.

Mandible with three teeth and a pectinated inner angle.

Maxilla I. with nearly straight edge distinctly marked. In the upper part a notch is situated, with a strong spine in the bottom.

Maxilla II with a spineless minute notch at the middle of the front edge. A posterior lobe with bristles is differentiated; behind this a minute maxillary lobe.

Measurements (in millimetres):—

Length of capitulum, 19·5.

Breadth of capitulum, 11.

Length of peduncle, 11.

Breadth of peduncle, 5.

Number of segments of the Cirri:—

I.	II.	III.	IV.	V.	VI.	Caudal appendage.
9 11	17 19	18 19	17 18	19 19	21 22	1

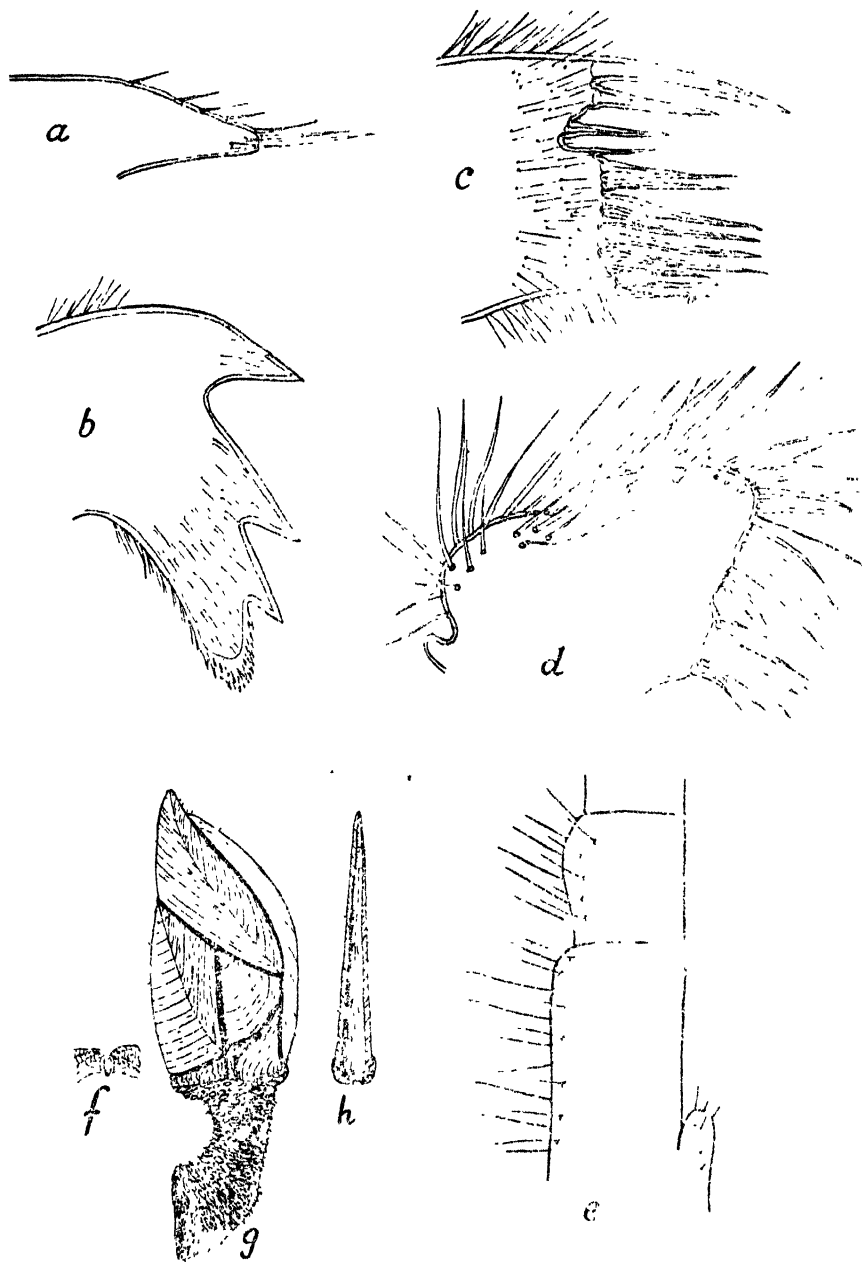
Cirrus I. with unequal rami. The longer cirri with rami of equal length. Up to five pairs of spines on the front edge of the segments. The *caudal appendages* are short, one-jointed, and distally rounded with short hairs.

Old locality. Galapagos Islands, lat. 36° 30' S., long. 89° 19' W., 634 fathoms.

New locality. Lat. 19° 26' S., long. 70° 27' W. (343–400 fathoms; C.S. 'Retriever'). Presented by Eastern and Associated Telegraph Companies.

Affinity. This species, according to Pilsbry, closely resembles *S. rathbuna* Pilsbry (1907 a) from the Atlantic coast of South America, which species also

TEXT-FIG. 3.

*Scalpellum soror* Pilsbry.

- a. Palpus. b. Mandible. c. Maxilla I. d. Maxilla II. e. Cirrus VI. and caudal appendage. f. Rostrum and rostral latera. g. The animal, lateral view. h. Carina and carinal latera.

I had the opportunity (1921) of re-identifying, and of giving descriptions of internal parts. Relationship also exists in the short one-jointed caudal appendages.

SCALPELLUM GRUVELIANUM Pilsbry, 1907. (Text—figs. 4, 5.)

Scalpellum gruvelianum Pilsbry (1907 a), (1907 b); Broch (1922).

Scalpellum gruvelianum secundum Pilsbry (1907 b); Broch (1922).

Scalpellum columbianum Pilsbry (1909).

Discussion and Complementary Description.

The material consisted of individuals of different ages, showing that variation exists among the single individuals. Broch (1922) describes also specimens of the typical form and of the subspecies *secundum*, and of forms intermediate between the two in the same material. My opinion based on this rich material is that Pilsbry's subspecies cannot be upheld as a subspecies but only as a forma *secundum* with more separated plates, a feature seen in many *Scalpellum* species. *S. columbianum* Pilsbry (1909) I must consider as only a young individual of *S. gruvelianum* which is also found, according to Broch, from British Columbia as *columbianum*. Reasons for this will follow in the complementary description.

Capitulum, in individuals here dealt with, is rather broad, as Pilsbry figured for *secundum*, but there are in this material also smaller individuals with a more elongated capitulum as in *S. columbianum* (length of capitulum 8.5 and 7.7 mm.). The plates are generally more separated in the older individuals, which Pilsbry says is a characteristic feature of the subspecies *secundum*; but this is no character of value, as this material also contains specimens of the same size without much separated valves. Characteristic of the species are the boundary-lines in the chitin between the plates. Occludent margin of the capitulum nearly straight or a little arched, but the carinal margin is strongly arched.

Scutum quadrangular with occludent margin nearly straight and sometimes, especially in smaller individuals, arched. The apical umbo is a little recurved. No important differences exist here from the above-mentioned species.

Tergum triangular with an arched occludent margin. The basal margin nearly straight.

Carina very long, regularly arched, with an apical umbo, as a rule extending very high up between the terga. The sides well developed, sometimes a little wider above. The dorsal roof very narrow bordered by wide rounded ribs. In this respect the species is differentiated from the allied *S. soror* collected together with this.

Upper latus quadrangular to pentagonal with the lower corner rounded. The shape is consequently variable. In individuals with separated valves the plate may be narrower. In full-grown individuals the umbo is situated a little beyond the apex, with ridges from the nearest corners—which is not mentioned in the earlier descriptions.

Rostrum very minute, reduced. Pilsbry mentions for the type of *S. gruevelianum* no rostrum, but later (1907 *a*) he found one.

Rostral latus very wide, which distinguishes the species from many others nearly related, as *S. sanctipetrense* Pilsbry, 1907 *a*, and *novæ-zelandiæ* Hoek, 1883.

Inframedian latus narrow, somewhat variable in shape. Originally the plate is of the hour-glass shape, but in smaller but mature individuals in this material it is nearly triangular, with the umbo subapical. By development of the secondary part of the plate the umbo at last becomes subcentral to central. In Pilsbry's individuals the umbo is subapical in the typical form, central in subspecies *secundum*, and finally in *columbianum* subcentral, as in most of my individuals here.

Carinal latus high with the umbo near the basis of the carina projecting a little beyond the carina. The lateral and carinal margin as a rule separated, but sometimes with an indistinct corner. Basal margin straight. The plate is very like that of *S. retrieveri*, sp. n., there being some differences, however.

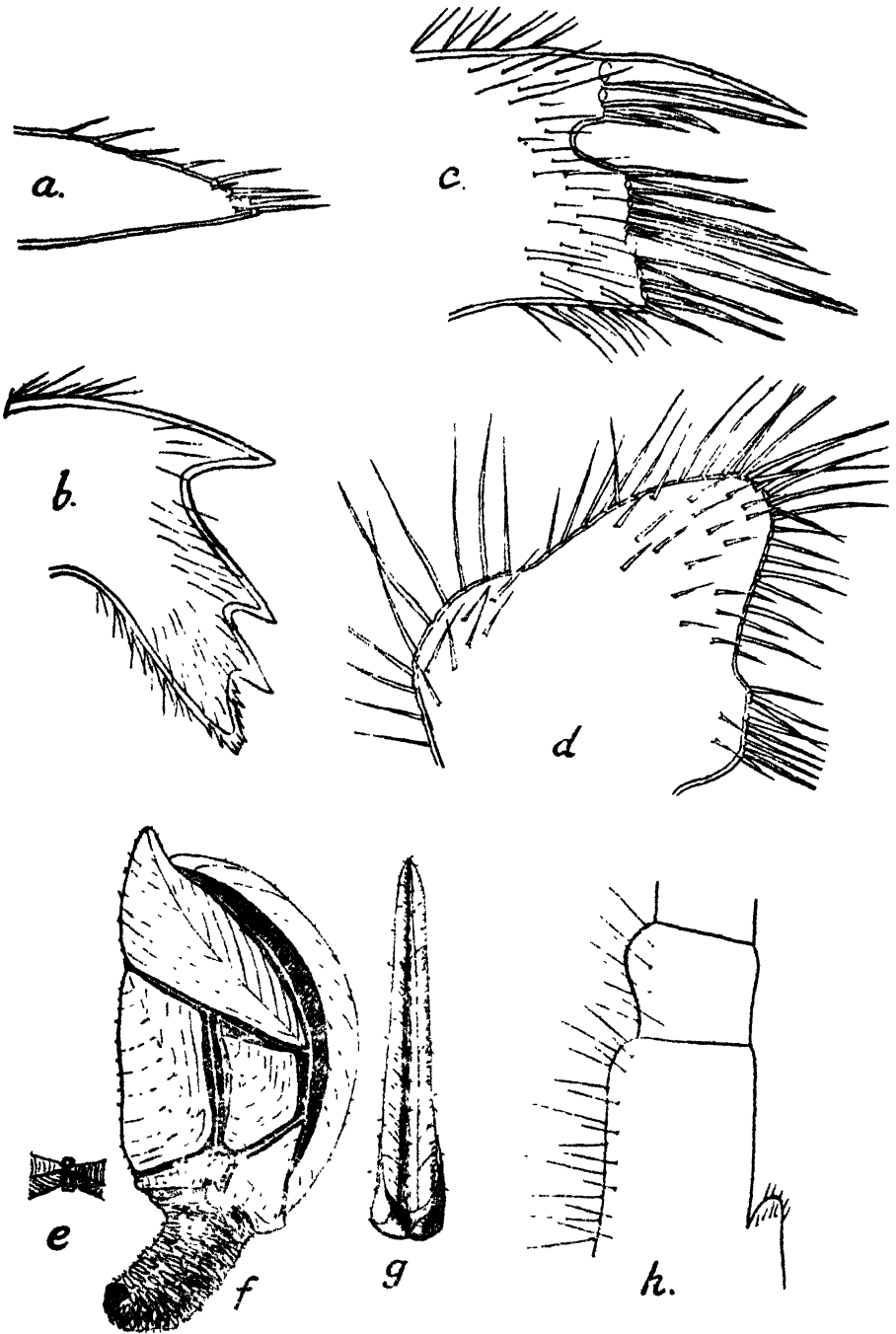
Peduncle shorter than the capitulum, but variable in length on account of different contractions. Scales wide with distinct interspaces. The younger individuals often have few scales.

Of this species, which was most richly represented in this collection, four *very young specimens* were also found, situated on the older individuals. I think, to judge from the shape of the valves, there can be no doubt that they belong to *S. gruevelianum*, although there were three other species taken together with this, but only represented by single individuals. Unfortunately, no *cypriis* stages with incipient development of the valves were met with; yet it may be of interest to figure the examples found (text-fig. 5), as very little is known about young stages of Cirripedes. Broch has described and figured some younger individuals of *S. scalpellum* (L.) and *S. stræmii* M. Sars, and also (1922) two stages of this species, f. *secundum*. He has stated that the plates of the capitulum appear in a definite succession—different on the one hand for *S. stræmii* and on the other hand for *S. scalpellum* and *S. gruevelianum*. Broch (1924, p. 21) says about this:—"Welche Bedeutung diesen Unterschieden beizumessen ist, muss vorläufig dahin gestellt bleiben. Dazu ist bisjetzt die Entwicklung der Skelette der meisten *Scalpellum*-Arten zu wenig untersucht worden." By comparison between my stages and Broch's of *S. gruevelianum* it seems to me that some variability in this succession exists.

In my youngest individual (text-fig. 5, *a*, *b*), which has not lost the antennæ, all valves of the capitulum except rostral latera are developed. It is of interest to see that the rostrum, which in adult specimens is rudimentary or absent, is rather large in this small individual. In Broch's specimens of this species the rostrum is formed in a later stage, and so after the other plates in the nethermost row. Of the peduncular scales two pairs are already formed, the stage being much like that figured for *S. scalpellum* (Broch, 1924, fig. 4, *d*).

In the next stage (text-fig. 5, *c*, *d*) the rostral latera begin to develop, but they are still very small. The rostrum is a little smaller than in the preceding

TEXT-FIG. 4.



Scalpellum gruvelianum Pilsbry.

- a. Palpus. b. Mandible. c. Maxilla I. d. Maxilla II. e. Rostrum and rostral latera. f. The animal, lateral view. g. Carina and carinal latera. h. Cirrus VI. and caudal appendage.

stage, but no new scales on the peduncle appear. In the latest stage (text-fig. 5, e, f) all plates have grown and the rostral latera are now larger than the rostrum, which has become smaller and more rounded than before. It is of interest to find that new scales on the peduncle appear above the older at the transition from the capitulum to the peduncle, as Broch has already stated. The primordial valves of the scutum, tergum, and carina seem to be smaller in the older stages. In all the present specimens the two tentacular appendages at the apex of the capitulum are found. Broch did not find such appendages in the youngest individual. He speaks of the probability that his youngest stage may belong to another species, but does not deem it likely. If the latter is the case we have to count with a great degree of variability in younger stages. I do not think it possible that my stages can belong to any other species.

In this connection it may be mentioned that Broch has based his phylogenetical view that *Scalpellum* and other forms with large number of plates are derived from an ancestral form with five plates, on the fact that the first stages of *Scalpellum* and other Cirripedes have five valves, and not until later on do the others begin to appear. I think he has taken too little heed of the paleontological facts when he (1927, p. 544) says:—"Die geologischen Daten geben uns überhaupt bis jetzt ausserordentlich zweifelhafte Anhaltspunkte für eine kritische Beurteilung der Abstammung der Ordnung." Recently (1928) a very interesting work by Withers has appeared. In it he discusses the phylogeny from many points of view, especially that of paleontology, and shows that everything argues for the development of later Cirripedes from forms with many valves to such with few as, e.g., *Lepas*. But he adds that the earliest-known fossil Cirripede has six valves. It seems, consequently, quite right, as is pointed out in this paleontological work, that the phylogeny cannot possibly be explained only by ontogenetic facts which at present are not thoroughly elucidated. There is no reason, nor is it possible here, to discuss these comprehensive questions. As regards the genus *Scalpellum* more material of younger stages must be studied. It is often the case that the cenogenetic disorders in the ontogenetic development are so great that we cannot discover the phylogeny from that alone. It looks as if the stages above described, when compared with those of Broch, show us just such variations, though they are slight, with regard to the time of the appearance of the valves.

Mouth-parts are not described in the original descriptions; but, later, figures are given by Broch (1922) of the mandible and the maxilla I.

Labrum concave with teeth.

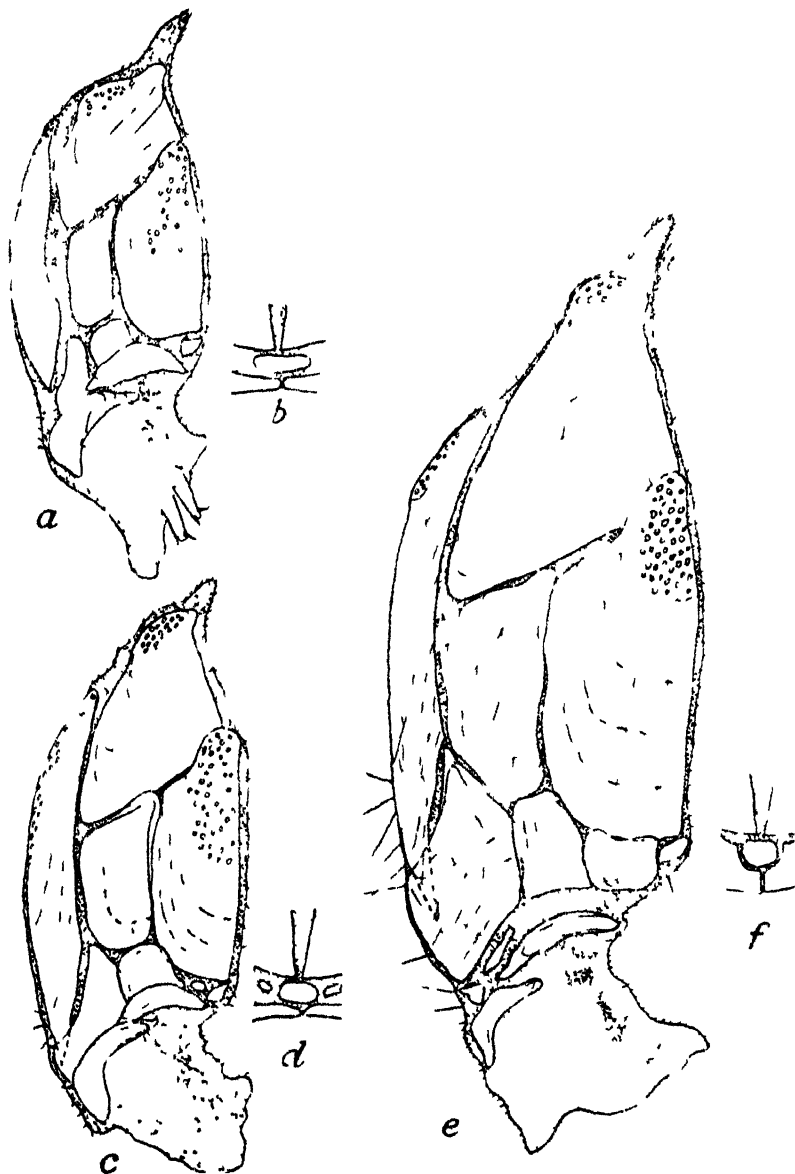
Palpus conical, with bristles at the end and the upper edge.

Mandible with three teeth and a pectinated inner angle.

Maxilla I. in these animals with a straight edge and a very distinct notch in the upper part, without spines. In the specimens described by Broch no such notch is mentioned; in these respects, therefore, variation exists.

Maxilla II. with a slight notch on the front edge. A posterior lobe is differentiated. Behind this a small maxillary lobe is situated.

TEXT-FIG. 5

*Scalpellum gruevianum* Pilsbry.

Young specimens. *a.* 1.46 mm. in length. *b.* Rostral part of the same. *c.* 1.52 mm. in length. *d.* Rostral part of the same. *e.* 2.37 mm. in length. *f.* Rostral part of the same.

Measurements (in millimetres) :—

Length of capitulum, 20, 6.5, 20.

Breadth of capitulum, 12, 3.5, 12.5.

Length of peduncle, 6, 3, 14.

Breadth of peduncle, 5, 1.5, 5.5.

Number of segments of the Cirri :—

I.	II.	III.	IV.	V.	VI.	Caudal appendage.
9 11	15 16	16 16	17 19	17 18	18 19	1
7 8	10 11	14 14	14 15	16 16	14 15	1

The smaller number of the segments of the longer cirri (13) in Broch's individuals can be explained, as the individuals are younger ones. The *caudal appendage* is short, one-jointed, with very short bristles, as is also stated by Broch (1922, fig. 7, f).

No *penis*.

Complemental male sack-like, without traces of plates, as Broch also mentions.

Old localities. California, Santa Barbara Island, South-west Rock, 238 fathoms (*S. gruvelianum* Pilsbry, 1907 b).—Southern California, 269, 603 fathoms (*S. gruvelianum*, Pilsbry, 1907 a).—British Columbia, Strait of Georgia, 50 and 40 fathoms, Naraimo, Departure Bay, 20 fathoms (*S. gruvelianum* Broch, 1922).—Southern California, Santa Cruz Island, Gull Inlet, 506 fathoms (*S. gruvelianum secundum* Pilsbry, 1907 b).—British Columbia, Lowe Inlet, Burrard Inlet (*S. columbianum*, Pilsbry, 1909).

New locality. Lat. 19° 26' S., long. 70° 27' W. (343–400 fathoms; C.S. 'Retriever'). Presented by Eastern and Associated Telegraph Companies.

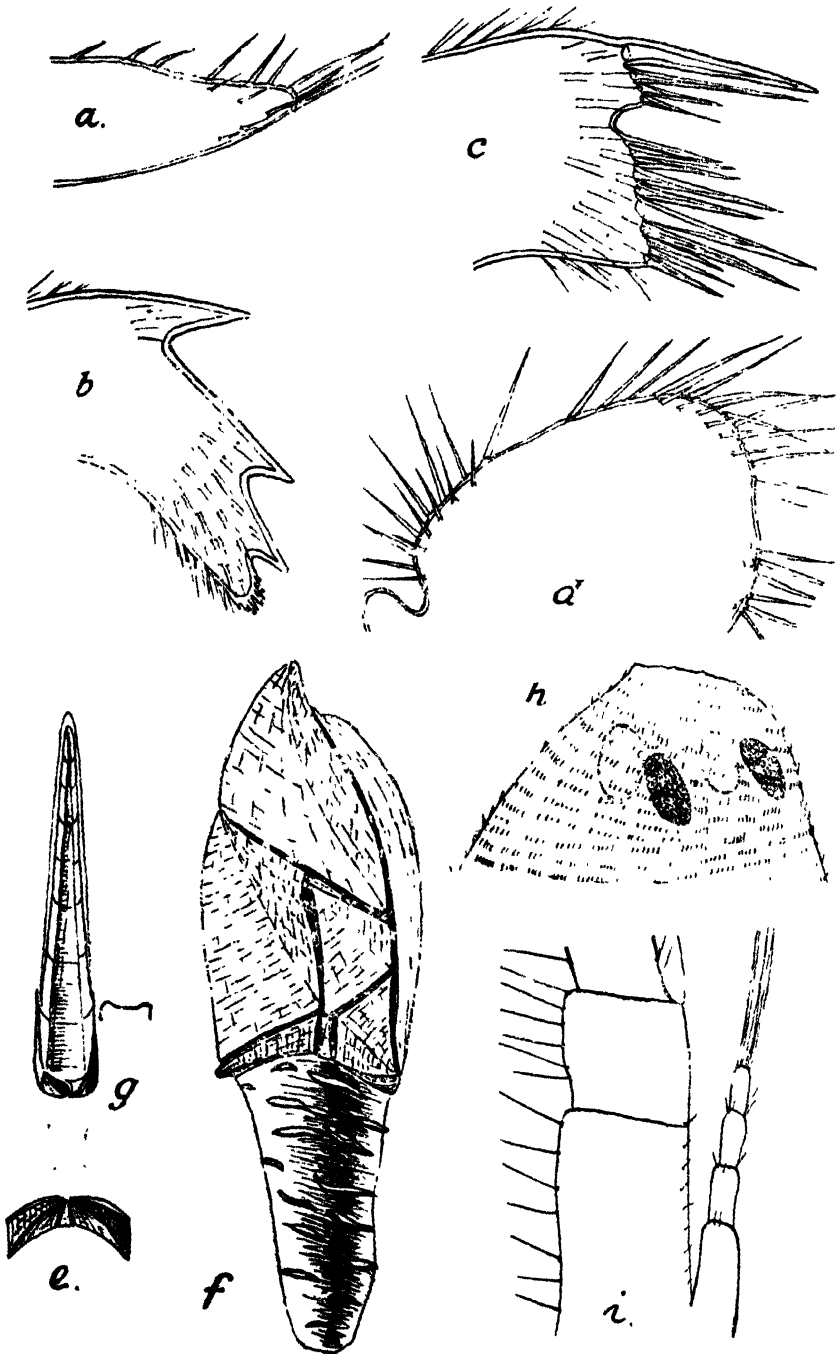
Distribution. West coast of North and South America, 20–603 fathoms. The distribution is not continuous, as localities are lacking from the middle or tropical part (Mexico and Northern South America). This may be due to our imperfect knowledge of such forms, especially from this part of the ocean. It is also possible that *S. gruvelianum* represents a stenotherm species preferring colder waters. If the species is a boreal one, as Broch (1922) supposes, it is interesting to note that it is now also mentioned from the coast of Chile, which is influenced by the cold Peru stream. Judging from the localities, most of the specimens are taken from deep waters. Only the northern localities from British Columbia belong to the littoral, *sensu stricto*. A possibility is that the localities from the north and south parts of the American coast can be connected in the greater depth of the middle warmer part.

SCALPELLUM RETRIEVERI, sp. n. (Text-fig. 6.)

Holotype; in the British Museum (Natural History), London.

Diagnosis. Female: capitulum with 14 plates with small interspaces and a thin cuticle. Scutum quadrangular with convex occludent margin. Carina long, regularly arched, with the umbo subapical; the roof slightly concave

TEXT-FIG. 6.



Scalpellum retrieveri Nilsson-Cantell, sp. n.

- a. Palpus. b. Mandible. c. Maxilla I. d. Maxilla II. e. Rostrum and rostral latera.
 f. The animal, lateral view. g. Carina and carinal latera. h. Part of the complementary male with four plates. i. Cirrus VI. and caudal appendage.

with narrow ridges. Upper *latus* quadrangular with subapical umbo. Rostrum very minute. Rostral *latus* very low with projecting umbo. Inframedian *latus* narrow; umbo subapical. Carinal *latus* high with the umbo nearly basal, not projecting; lateral and upper margins well defined. Peduncle shorter than the capitulum; scales transversely elongated, well separated. Mandible with three teeth and a pectinated inner angle. Maxilla I. with a deep notch without spines. Maxilla II. with bristles in three groups; maxillary lobe small. Caudal appendage 4-jointed, longer than the proximal segment of the protopodite. Complemental male sack-like with four plates; without cirri; surface with small spines in groups.

Discussion and Description. This species is represented by one mature specimen. It was found together with *S. gruvelianum*, which is a very closely-related species. The external differences are yet great enough to distinguish them. Also in the internal parts there are differences between the two, as, e. g., in the caudal appendages.

In the literature I find many allied species unfortunately imperfectly described. Some of them, as *S. trapezoideum* Hoek, 1907, *S. bouveri* Gruvel, 1906, *S. tenue* Hoek, 1883, *S. ventricosum* Hoek (1907), 1913, differ especially from this specimen in having a higher rostral *latus*. Another species, *S. incisum* Aurivillius, 1898, from the Atlantic Ocean (re-described but imperfectly, as internal parts are not mentioned, by Gruvel, 1920) affords external similarities, but in other respects I think it is differentiated from this specimen from the Pacific Ocean. The most related species is, I think, *S. intermedium* Hoek, 1883, also from the Pacific Ocean. This species has generally some reduced plates, but in 1921 I also found a smaller specimen of *S. intermedium* with wholly calcified plates very like this. I was at first inclined to describe the specimen under review as belonging to this species, but on comparison with the Swedish material of *S. intermedium* I find some differences, as will be shown in the following description, which give grounds for keeping it separate.

Capitulum with 14 plates, well calcified with small chitinous interspaces and a very thin and not hairy cuticle. The striation on the plates is indistinct.

Scutum quadrangular with ocludent margin convex. Lateral margin concave in the upper part.

Tergum triangular with ocludent margin convex. The basal margin is nearly straight.

Carina regularly arched with the umbo subapical. The sides well developed. The roof is flat, rather wide below, bordered by narrow but distinct ridges.

The upper *latus* quadrangular with distinct corners. Situation of umbo subapical. In younger specimens, I think, apical.

Rostrum very much reduced, with its greatest extension in the same direction as rostral *latera*.

Rostral latus very characteristic for this species, as it is very low and long, with the umbo projecting. Distinct ridges from the umbo to the opposite corners.

Inframedian latus narrow, elongated, with the umbo subapical in this specimen, but, I think, apical in younger individuals. These two later plates different from those in *S. intermedium*.

Height of the *carinal latus* twice the width. The umbo near the base, not projecting beyond the carina as in *S. intermedium*. The lower part of the carinal margin is very short. The latera and upper margins are straight.

Peduncle shorter than the capitulum with narrow transversely elongated scales sparse in number. Whether this is due to age it is not possible now to decide. Often younger individuals of *Scalpellum* have fewer plates than older ones. The smaller specimens described by me (1921) as *S. intermedium* have densely placed scales. *S. intermedium* is thus a species of smaller size.

Mouth-parts. *Palpus* conical with bristles at the end and the upper side.

Mandible with three teeth and a pectinated inner angle.

Maxilla I. with straight front edge. A very distinct notch in the upper part of the edge as in *S. intermedium* (Nilsson-Cantell, 1921, text-fig. 33, b).

Maxilla II. with bristles in three groups, as the front edge has a middle part without bristles. Behind the posterior group a maxillary lobe is situated.

Measurement (in millimetres) :—

Length of capitulum, 13.

Breadth of capitulum, 7.5.

Length of peduncle, 9.

Breadth of peduncle, 3.5.

Number of segments of the Cirri :—

I	II.	III	IV.	V.	VI.	Caudal appendage
7 10	15 16	— 20	21 22	22 23	— 22	5

Cirrus I. with short unequal rami. Cirrus II. shorter than the following with rami equal as in the others. The longer cirri with four pairs of spines on the front edge of the segments.

The *caudal appendage* short, a little longer than the proximal segment of the protopodite. In *S. intermedium* the appendage is shorter than the segment. This must be further proved from richer material. The number of the segments for both species nearly the same.

No *penis*.

Complemental males were found on the inside of the scuta. The two males were in a bad condition, as is often the case after preservation. The male is of the sack-like type with prehensile antennæ near the one pole. At the opposite pole four small reduced valves are placed round the mantle-opening. The male is very like that figured by Gruvel (1902) for *S. luteum*; the surface is covered by very small transversely grouped spines, and muscle-fibres of the sack are distinct. The male is different from that of *S. intermedium*, as it is

more reduced. This species has four small valves and segmented cirri protruding from the mantle-opening.

Locality. Lat. $19^{\circ} 26'$ S., long. $70^{\circ} 27'$ W. (343–400 fathoms; C.S. 'Retriever'). Presented by Eastern and Associated Telegraph Companies.

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Asellus cavaticus Schiödte, a blind Isopod new to the British Fauna, from a well in Hampshire. By WALTER M. TATTERSALL, D.Sc., Professor of Zoology, University College, Cardiff. (Communicated by Dr. W. T. CALMAN, F.R.S., F.L.S.)

(PLATE 6, and 3 Text-figures.)

[Read 15th November, 1928.]

IN 1925 the British Museum received specimens of an *Asellus* collected by Miss Lucas from a well at Ringwood, Hampshire, which proved on examination to be a blind species near to, if not identical with, *A. cavaticus* Schiödte, and certainly new to the British fauna. Further specimens were sent at intervals between March 1925 and January 1926. I am indebted to Dr. W. T. Calman, F.R.S., for the opportunity of examining these specimens and for permission to describe them. I think they are certainly identical with *A. cavaticus* Schiödte, a subterranean species not infrequently met with in caves and wells on the Continent, and it is a matter of great interest that it should now be found in a similar situation in this country. Now that attention has been drawn to its occurrence, further search will doubtless reveal a wider distribution in suitable locations in Great Britain.

The species, *A. cavaticus*, is still somewhat shrouded in obscurity. Fairly good descriptions have appeared by Fries (1879) and Miethe (1899), and it has been the subject of a great many odd notes and records from time to time. In the light of recent work by Racovitza, Monod, and Dudich, in the course of which many new species and varieties of *Asellus* have been described, it seemed desirable to re-describe and figure *A. cavaticus* and to attempt to unravel its history. This I have tried to do in the following paper. I have given a somewhat lengthy and, I hope, complete account of the history of the species, a re-description with figures of the essential parts, and some notes on its geographical distribution. Miss Lucas is to be congratulated on the discovery of so interesting an addition to our fauna. I am greatly indebted to the authorities of the British Museum and to Dr. Calman for permission to study these specimens, and to my wife for the drawings which accompany this paper.

HISTORICAL.

In 1849 Fuhlrott figured, but did not name, an *Asellus* from a well at Elberfeld, and, in the brief description which accompanied the figure, there is no mention of any specially distinctive characters which would enable the species to be definitely identified. Later authors have generally regarded the species found by Fuhlrott as that which was subsequently named *A. cavaticus* by Leydig and others, and *A. sieboldii* by de Rougemont.

In 1864 Quenstedt found specimens of an *Asellus* in the Falkensteiner Höhle which he referred to as "einer Zarter Isopode, durchsichtig wie glas, mitt schwarzen Darmkanal." Leydig (1867) examined a dried and somewhat damaged specimen sent to him from the same locality by a collector, Herr Brauer, and noted that it was without eyes and therefore essentially belonged to the Cave Fauna. Leydig later acquired numerous well-preserved specimens from the Falkensteiner Höhle, but, in the meantime, Dr. Meinert visited the locality and collected a large number of specimens which he handed to Professor Schiödte at Copenhagen.

Leydig (1871) made reference to these facts and stated that, in a letter he had received from Schiödte, the latter intimated his intention of describing the *Asellus* from the Falkensteiner Höhle as a new species under the name *A. cavaticus*. In these circumstances Leydig abandoned any idea of describing the species himself, preferring to await the promised description by "der Meisterhand des Entomologen in Copenhagen." This is the first published record of the name *A. cavaticus*.

Wiedersheim (1873) and Fries (1874) make further reference to this *Asellus*, in both cases from the Falkensteiner Höhle, under the name of *A. cavaticus*, without, however, giving any description—probably in view of Schiödte's promised description. Wiedersheim quoted a letter from Leydig saying that he had discovered Fuhlrott's figure of the *Asellus* from Elberfeld, and that it represented the same species as the one from Falkensteiner Höhle.

Schiödte's description never appeared, and the name *A. cavaticus* remained a *nomen nudum* until 1879, when Fries described the species in some detail without, however, giving any figures.

In the mean time, de Rougemont (1879) read a paper on "La faune des eaux privées de lumière" before the Natural History Society at Neuchâtel, and in the Proceedings of that Society, published in the same year, a brief *résumé* of his paper appeared in which he gave the name *A. sieboldii* to a blind *Asellus* found in wells at Munich. He was fully aware of the Falkensteiner Höhle discovery, for he referred the latter specimens to his species, apparently deciding that *A. cavaticus* was a *nomen nudum*. In his preliminary note de Rougemont gave the distinguishing characters of *A. sieboldii* as more elongated than *A. aquaticus*, without eyes and with the olfactory filaments very much developed.

De Rougemont's full paper was published first as a thesis at the University of Munich (1875), and later by the Natural History Society of Neuchâtel (1876). His final description of *A. sieboldii* was not very detailed, and gave very little additional information as to the way in which it differed from *A. aquaticus*. He completely overlooked the marked differences in the form of the pleopods in both sexes.

Leydig (1878) gave a few notes on *A. cavaticus* and the differences between it and *A. aquaticus*, but did not attempt a full description.

Forel (1878), in a brief paper on his work at Lake Geneva, announced the discovery in that lake of a blind *Asellus* which he referred to *A. sieboldii*.

apparently on the advice of de Rougemont. This *Asellus* was subsequently (Blanc, 1879) shown to be different from the cave species and was described under the name of *A. forelii* Blanc, and the differences between the two species tabulated.

Fries (1879) found *A. cavaticus* in the Hilgershäuser Höhle and gave a very good description of the species, unfortunately unaccompanied by figures. He showed that the differences in the antennules and antennæ given by Leydig to distinguish *A. cavaticus* from *A. aquaticus* do not hold when a large number of specimens is examined. He described accurately the differences between the pleopods of the two species, and rightly emphasised the value of this character as of specific importance.

In the same year Weber (1879) found specimens in a well at Bonn, and, independently of Fries, described the differences between *A. cavaticus* and *A. aquaticus*. The accounts given by Fries and Weber are in substantia agreement and supplement one another in minor points.

Weber (1881) quoted *A. cavaticus* and *A. forelii* as instances of the effects of darkness on animals, but added nothing to the descriptions already given.

Asper (1880) recorded *A. forelii* from the Vierwaldstättersee, and in the course of his remarks noted that he had obtained a single specimen of a blind *Asellus* from the University well at Zürich which closely resembled the Lake Geneva form. This specimen in all probability should be referred to *A. cavaticus*.

Dybowski (1884) and Bovallius (1886) include this species in their surveys of the genus under the name *A. sieboldii* de Rougemont.

Schneider (1888), in describing a new variety of *A. aquaticus* from underground waters near Freiburg, compared it with *A. cavaticus* and gave a figure of the first pleopod of the female of the latter for comparison with his new variety.

Hamann (1896) regarded *A. forelii* and *A. cavaticus* as one and the same species. He also records the finding of a specimen at Cerna jama in Carniolia which he refers to *A. cavaticus*, but there is nothing in his notes from which to form any opinion as to its identity. Racovitza (1925) has noted a new variety of *A. aquaticus* from this locality, *A. aquaticus cavernicolus*, and it is to this variety that Hamann's specimen should in all probability be referred.

Studer (1899) recorded *A. cavaticus* from Madretsch bei Biel, Canton Berne, Switzerland, and Miethe (1899) gave a detailed description of the specimen found by Studer. His figures agree substantially with my own, and I think we are dealing with the same species.

Carl (1908) gave a brief but accurate summary of the differences between *A. aquaticus* and *A. cavaticus*, and regarded *A. forelii* as a variety of the latter. He gave a very good bibliography and a full synonymy, but it is not clear that he actually examined specimens.

Kühne (1921) recorded *A. cavaticus* from a well in Kreise Holzminden.

Chappuis (1922) merely mentions this species as a member of the underground fauna from near Basel, referring to the earlier papers of Miethe and de Rougemont.

Racovitza (1923), in an essay on the morphology and phylogeny of the pereopods and their "phanères" figures the propodus and "organ dactylien" of *A. cavaticus*. In a later essay on the antennal flagellum the same author gives a detailed description of that appendage in *A. cavaticus* from a cave in Isère, France. He regards *A. cavaticus* as an isolated and primitive form.

Dudich (1925) divides the genus *Asellus* Geof. into two subgenera, *Asellus*, s. str., and *Proasellus* nov. The type-species of the latter subgenus is named as *A. meridianus* Rac., and *A. cavaticus* is listed among the species assigned to this new subgenus. The main points on which the new subgenus is founded are :—

- (1) The presence of five spines on the inner lobe of the first maxilla.
- (2) The absence of apophysis on the propodite of the second thoracic limb of the male.
- (3) The form of the pleopods in both sexes.

Spandl (1926) and Chappuis (1927), in works dealing with underground faunas, include *A. cavaticus* among the subterranean species.

ASELLUS CAVATICUS Schiödte.

Asellus sp. Fuhlrott, 1849

Asellus sp. Quenstedt, 1864.

Asellus sp. Leydig, 1871.

Asellus cavaticus (Schiödte, *in litt.*) Leydig, 1871; Wiedersheim, 1873; Fries, 1874; Leydig, 1878; Fries, 1879; Weber, 1879; Blanc, 1879 (1) and (2); Asper, 1880 (part); Weber, 1881; Schneider, 1888; Hamann, 1896 (part.); Studer, 1899; Mieth, 1899; Carl, 1908; Kuhn, 1921; Chappuis, 1922; Racovitza, 1923 and 1925; Dudich, 1925; Spandl, 1926; Chappuis, 1927.

Asellus sieboldii de Rougemont, 1875 and 1876; Dybowsky, 1884; Bovallius, 1886.

Nec *Asellus sieboldii* Forel, 1878 and 1879; Asper, 1880.

Locality. Wells at Ringwood, Hants, collected by Miss Lucas.

Material examined :—

One male and one female, collected March 2nd, 1925.

One female, collected April 13th 1925.

One male, collected June 1925.

Two males, collected January 1926.

Length of the largest specimen (a male) 8 mm.

Description. Body about four times as long as broad, of almost even width throughout; dorsal surface of the body rather sparsely clothed with scattered short setæ; lateral margins of the somites fringed with longer setæ.

Colour of preserved specimens white, without any trace of chromatophores.

Eyes absent.

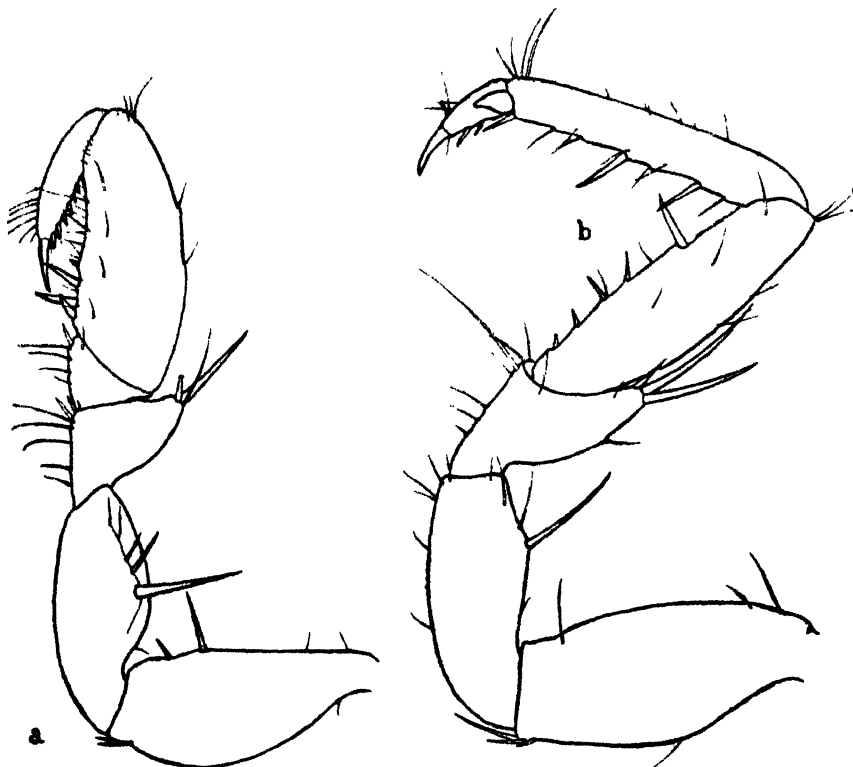
Antennules about two-thirds of the length of the peduncle of the antennæ; flagellum about equal to the peduncle, composed of nine or ten joints, the last joint very small; in the male, olfactory filaments are present usually on joints four to eight or nine; these filaments are about as long as the joints of the

flagellum, sometimes slightly shorter and sometimes slightly longer ; in one case a pair of filaments was present on the same joint ; in the female the number of olfactory filaments appears to be only three on joints 7 to 9.

Antennæ, when flexed backwards, extend to about the posterior end of the thorax or slightly beyond ; the last joint of the peduncle is about one-third longer than the penultimate ; flagellum composed of fifty to fifty-four joints.

The mouth-parts do not differ very considerably from those of *A. meridianus* Rac. The inner lobe of the first maxilla has five plumose setæ at the outer

TEXT-FIG. 1.



Asellus cavaticus Schiodte.

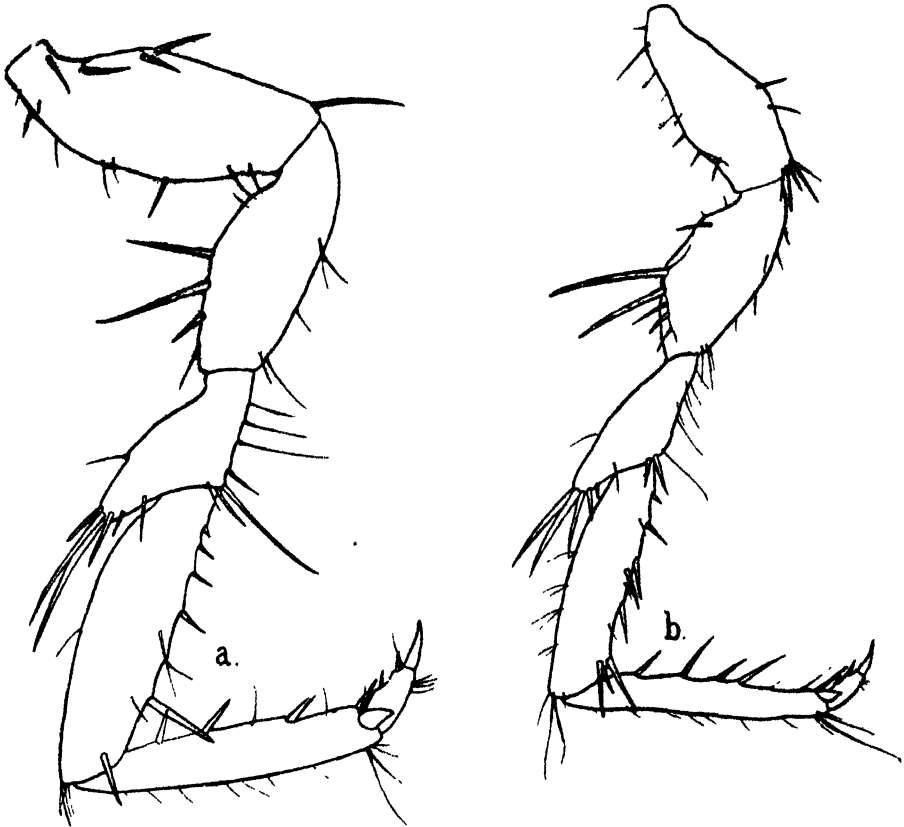
a. Second thoracic limb of the male, $\times 62.5$. b. Third thoracic limb of the male, $\times 62.5$.

distal end, and a single plumose seta on the lower face near the apex. The outer lobe is armed with thirteen barbed spines at the distal end and one supplementary seta. There is, in addition, a seta on the lower face. The maxillipeds have five masticatory hooks. I could not detect any difference between the maxillipeds of the male and female. In the two females at my disposal, which were both in the non-breeding phase, there is no trace of the coxal lobe characteristic of the female of *A. aquaticus* with fully-developed brood lamellæ.

The form of the pereopods is best described by reference to the accompanying figures of the first, second, fourth, and seventh pereopods of the male (text-figs. 1 and 2). The first pereopod (second thoracic limb) of the female is substantially the same as that of the male, there being no appreciable sexual difference such as is found, for instance, in *A. aquaticus*.

Abdomen about one-quarter of the length of the whole body, first and second segments distinctly marked off, posterior margin broadly rounded.

TEXT-FIG. 2.

*Asellus cavaticus* Schiödte.

a. Fourth thoracic limb of the male, $\times 62.5$. b. Eighth thoracic limb of the male, $\times 32$.

Uropods about equal or slightly longer in total length than the abdomen; sympod about as long as the exopod; exopod slightly shorter than the endopod; both rami tipped with two or three long setæ.

Second pleopod of the female (text-fig. 3 a) with the exopod twice as long as broad, inner margins almost straight, outer margin convex and armed with eight rather short plumose setæ; two simple setæ on the upper face of the appendage.

First pleopod of the male (text-fig. 3 *b*) with the sympod rectangular in shape, almost as long as broad, with two coupling-hooks on the inner margin. Exopod about twice as long as broad and twice as long as the sympod, with three simple setæ on the upper face, two near the proximal inner angle, and one more central, the distal and outer margins armed with about twenty-one setæ of varying size, the proximal eleven on the outer margin plumose, the remainder simple.

Second pleopod of the male (text-figs. 3 *c* and *d*) with the sympod one and a quarter times longer than broad, with the distal angles rounded and the internal margin armed with three short plumose setæ. Exopod only slightly more than half as long as the sympod, two-jointed, the proximal joint armed with one plumose seta on the outer margin, distal joint a little longer than broad, the outer margin furnished with seven short plumose setæ, the inner and distal margins with four plumose setæ. Endopod (text-fig. 3 *d*) modified as a copulatory organ, larger than the exopod, with a marked protuberance near the proximal end of the inner margin, cavity of the copulating organ opening at the apex of a recurved process with an open groove, beyond which the distal end of the joint is produced as an apophysial process.

The two females which I have examined are in the non-breeding phase when the four pairs of incubatory lamellæ, on the second to the fifth thoracic limbs (pereiopods 1-4), are very small and only just discernible. This fact may account for the apparent lack of sexual differences in the maxillipedes.

Remarks. Within the last few years, mainly owing to the researches of Racovitza, a large number of species of *Asellus* have been described from the fresh waters of Europe, Africa, and Syria. Two main groups of species can be recognized: the *aquaticus* group and the *meridianus* group, which Dudich proposes to distinguish as subgeneric groups, using *Asellus*, s. str., for the *aquaticus* series and *Proasellus* for the *meridianus* series. The full list of species and varieties as far, as I can make it out, is as follows:—

Asellus (Asellus) aquaticus Linn. Widely distributed in Northern Europe.

„ „ „ *fribergensis* Schneider. Freiburg.

„ „ „ *cavernicolus* Racovitza. Carniola.

„ „ *arthrobranchialis* Dudich. Near Naples.

„ (*Proasellus*) *meridianus* Racovitza. France, England.

„ „ *cavaticus* Schiödt. Germany, France, England, and Switzerland.

„ „ *forelii* Blanc. Swiss Lakes.

„ „ *cozalis* Dollfus. Syria.

„ „ „ *peyerimhoffi* Racovitza. Algeria.

„ „ „ *africanus* Monod. N. Africa.

„ „ „ *cyanophilus* Dudich. Syracuse.

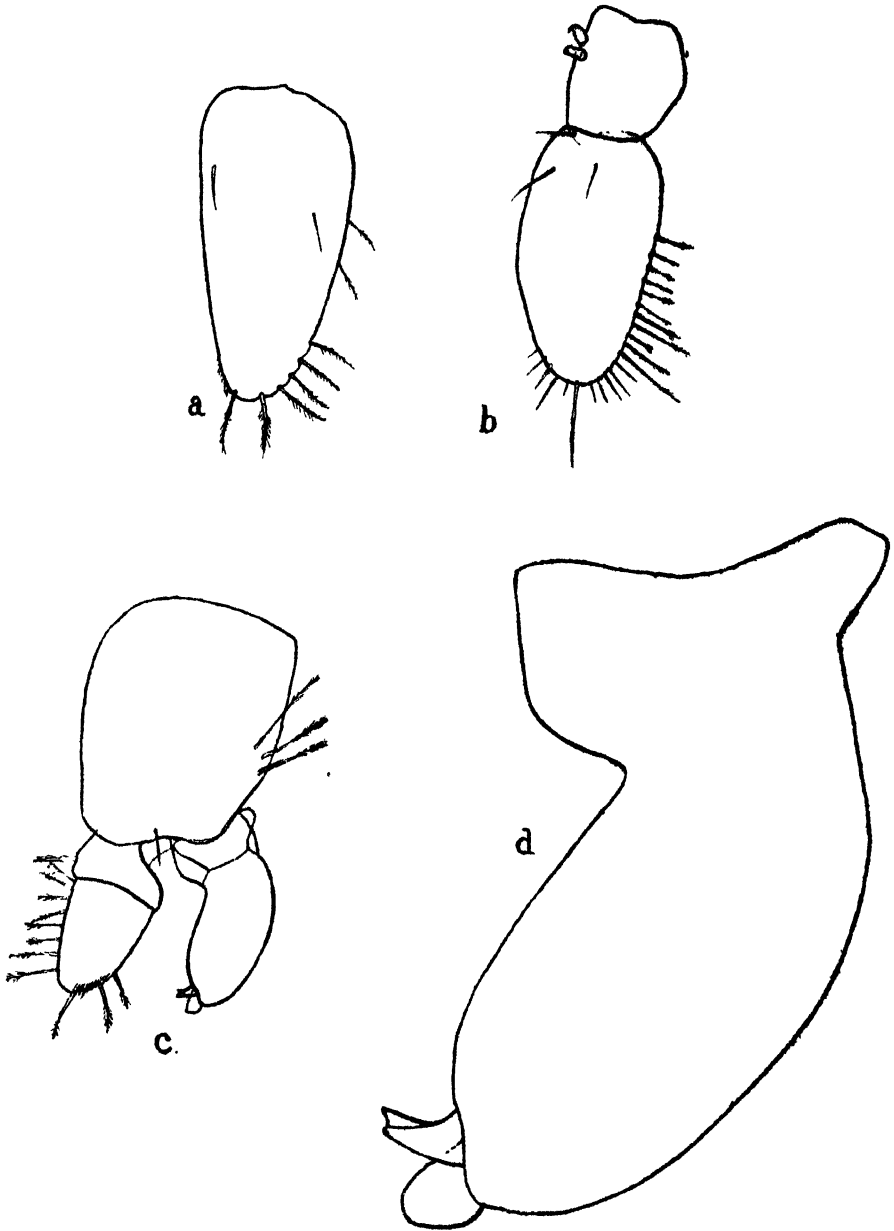
„ „ *banyulensis* Racovitza. Banyuls-sur-Mer.

„ „ „ *wolfi* Dudich. Syracuse.

„ „ sp. aff. *banyulensis* Racovitza. Denia, Spain.

„ „ *spelæus* Racovitza. Basses-Pyrénées.

TEXT-FIG. 3.

*Asellus cavaticus* Schiödte.

- a.* Second pleopod of the female, $\times 62.5$. *b.* First pleopod of the male, $\times 62.5$. *c.* Second pleopod of the male, $\times 62.5$. *d.* Endopod (copulatory organ) of the second pleopod of the male, $\times 240$.

Asellus (*Proasellus*) *spelæus aquæ-calidæ* Racovitza. Basses-Pyrénées.

„ „ *hypogeus* Racovitza. Algeria.

„ „ *gauthieri* Monod. Algeria.

„ „ „ *thermonyctophilus* Monod. Algeria.

„ „ *polychætus* Dudich. Near Naples.

„ „ *italicus* Dudich. Naples.

Of these species and varieties, six, all belonging to the *meridianus* group, are blind, viz. :—

A. cavaticus.

A. forelii.

A. spelæus.

A. spelæus var. *aquæ-calidæ*.

A. hypogeus.

A. gauthieri var. *thermonyctophilus*.

A. cavaticus differs from *A. forelii* as follows :—

1. In its larger size : 8 mm. against 5 mm.
2. In the greater length of the second antenna : $\frac{5}{6}$ of the body-length against $\frac{1}{2}$.
3. In the greater number of joints in the flagellum of the second antenna : 25–55 against 13–26.
4. In the longer flagellum of the first antenna : 6–12 joints against 5.
5. In the relatively longer olfactory filaments on the first antenna.

The differences between *A. cavaticus* and the remaining blind species are much less tangible and less easily expressed. Beyond a difference in size (*A. cavaticus* is 2 mm. longer than any of the other species), I can find no appreciable differences in the proportions of the body, in the relative lengths of the first and second antennæ, in the number of joints of the flagella of these appendages, and in the olfactory filaments on the first antenna. The published descriptions of these characters in all the species mentioned are in sufficient agreement with the conditions in *A. cavaticus*. The differences resolve themselves into minute differences in the proportions of the parts of the first and second pleopods of the male and in the second pleopod of the female, and in the number and character of the setæ arming these appendages.

A. cavaticus would appear to approach most closely to *A. hypogeus* Rac. in the shape and form of the endopod of the second pleopod of the male (copulatory organ). In these two species alone the cavity of the copulatory organ opens at the end of a recurved, somewhat hook-shaped process with an open groove. In the other species this process is apparently without the open groove.

A. cavaticus differs from *A. hypogeus* in the following points :—

1. In *A. cavaticus* there are two hooks on the sympod of the first pleopod of the male, while in *A. hypogeus* there is only one.

2. In *A. cavaticus* the twelve proximal setæ on the external margin of the exopod of the first pleopod of the male are plumose and the distal 11-12 setæ smooth, while in *A. hypogeus* the proximal twelve setæ are smooth and the distal 6-7 setæ are plumose.

3. In *A. cavaticus* the distal joint of the exopod of the second pleopod of the male is $1\frac{1}{2}$ times as long as broad, has 11-12 plumose setæ on its margins, and a pad of very short setæ on its tip, while in *A. hypogeus* the same joint is twice as long as broad, has two short simple setæ and seven longer plumose setæ on its margin, and no apical pad.

4. In *A. cavaticus* the apophysal process of the copulatory organ is shorter and stouter than in *A. hypogeus*.

The pleopods of the female in *A. hypogeus* are unknown, and consequently it is not possible to compare the species in this respect.

It is interesting to note that all the blind species and varieties exhibit the same modifications to an underground life, loss of eyes, absence of pigment, and greater development of the olfactory filaments on the antennæ. Moreover, all are associated with surface forms belonging to the same group, in which the eyes are developed and the body is pigmented.

Geographical area.	Surface forms	Associated subterranean forms
Germany, France, Switzerland. Great Britain.	<i>A. meridianus</i> .	<i>A. cavaticus</i> (wells, caves).
		<i>A. forelii</i> (deep water, Swiss lakes).
Pyrenees.	<i>A. banyulensis</i> .	<i>A. spelæus</i> .
North Africa.	<i>A. coralis</i> .	<i>A. hypogeus</i> .
		<i>A. gauthieri</i> .

Distribution.—*A. cavaticus* has been recorded from the following localities in Europe :—

GERMANY.		
Elberfeld (wells).	Fuhlrott.	Middle Devonian.
Munich (wells).	Rougemont.	Oligocene, Quaternary.
Falkensteiner Höhle.	Leydig.	Jurassic.
	Wiedersheim.	
	Fries.	
Hilgershäuser Höhle.	Fries.	
Bonn (wells).	Weber.	Oligocene, Quaternary.
Kreise Holzwinden.	Kühne.	Triassic.
FRANCE.		
Isère.	Racovitza.	Quaternary.
SWITZERLAND.		
Zurich (wells).	Asper.	Miocene, Quaternary.
Madretsch bei Biel (Canton Berne).	Studer.	Miocene, Quaternary.
Basle.	Chappuis.	Oligocene, Quaternary.
GREAT BRITAIN.		
Ringwood, Hants (wells).		Eocene (Bagshot and Brocklesham Beds).

The species has not been hitherto recorded from the British Isles, and further search for it is highly desirable. It is doubtless more widely distributed in this country in suitable localities.

In the above list of records I have indicated the geological formation in the localities in which the species were found, as far as I could trace it on a somewhat small-scale geological map of Europe. I cannot pretend that this geological information is absolutely accurate; but, such as it is, it suggests the preponderating association of this species with tertiary and quaternary deposits. This suggestion becomes more emphasised by a glance at the geological map of Europe, on which the occurrences of this species are plotted. It is found in the quaternary plain of the Rhine up to Basel, and on the tertiary and quaternary belt which extends from Geneva to Regensburg in South Germany and includes the Swiss Lakes. It is also recorded from the south-western extension of this belt into South France. The recorded occurrences of this species from the primary and secondary rocks surrounding these tertiary and quaternary plains are at present much fewer. The data are much too scanty to do more than suggest that the apparent association of this species with tertiary and quaternary deposits is a matter which might yield interesting results if extended observations were undertaken.

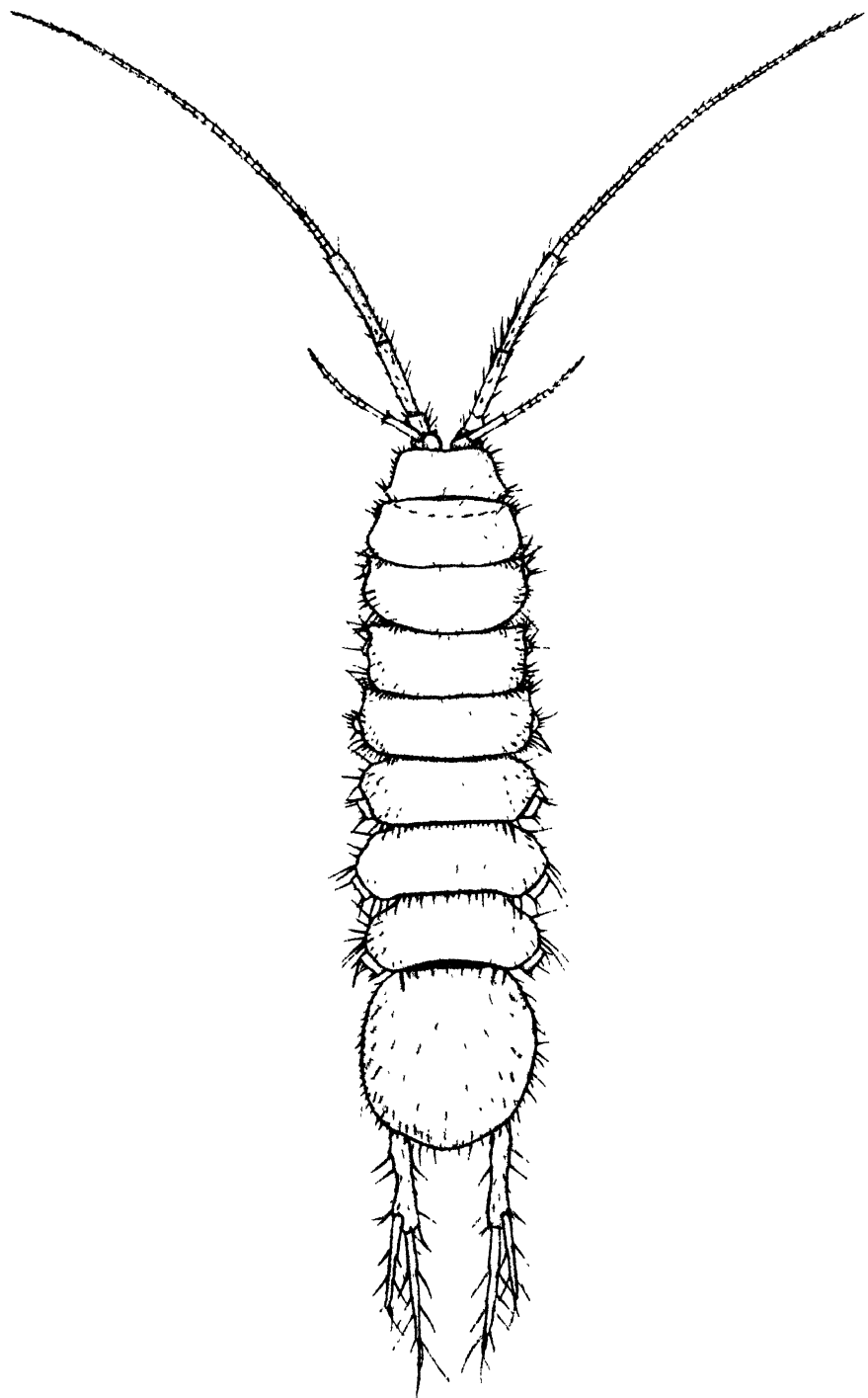
It may be further pointed out in this connection that the whole *meridianus* group of species appears to have a distribution largely coinciding with that of the tertiary and later formations. *A. coxalis* and its varieties are widely distributed over the great tertiary and quaternary belts of North Africa, extending into Syria; *A. banyulensis* and its varieties are found on the same deposits in S. France and Spain; *A. hypogeus* on the Eocene of Algeria; *A. gauthieri* on the Miocene and quaternary of Algeria; and *A. italicus* from the quaternary diluvium in the neighbourhood of Naples. *A. speleus* alone seems to be entirely associated with earlier geological formations, the Silurian and Cretaceous rocks of the Pyrenees region.

The suggested association of species of the *meridianus* group with tertiary and later deposits applies least to *A. meridianus* itself. This species is widely recorded in France and Great Britain, in localities whose geological formations vary from Lower Old Red Sandstone to Oligocene. *A. meridianus* is regarded by Racovitza as one of the more recent, more highly-evolved of the *meridianus* group, and, if so, it probably represents a more virile and adaptable species which has lost its association with tertiary and later deposits and has adapted itself to a wider range of localities. On the other hand, *A. meridianus* lives in that part of Europe which has been most extensively and intensively studied; and herein may be found the explanation for the want of correlation between its occurrence and the tertiary deposits, so much more marked in other forms. Equally extensive and intensive work in other parts of Europe and Africa may show that there is nothing in the suggestion I have made, and that the correlation between organism and geological formation is a mere coincidence.

I would remark, finally, that the occurrence of *A. cavaticus* in Great Britain is interesting from another point of view. It must have been isolated in this country from at least as long ago as the glacial period, and yet it appears to have survived practically unchanged since that time. As far as I am able to judge from published descriptions and figures, the Hampshire specimens belong to the same species as those collected in Germany, France, and Switzerland at the localities detailed above. A re-description of Continental specimens of this species in the light of recent knowledge has been promised by Racovitza, but has not so far appeared. At the moment, therefore, I can see no grounds for supposing that isolation in Britain has led to the development of any characters of specific value, in the absence of first-hand comparison with specimens from abroad. This is, perhaps, only to be expected when it is considered that the conditions under which this species lives are probably more constant than in any other environment—at any rate, as regards such fundamental factors as absence of light and temperature of the water are concerned. Isolation for long periods under such constant conditions has failed to induce any appreciable modifications of structure. This receives some measure of support from the opinion of Racovitza that *A. cavaticus* is one of the more primitive species of the *meridianus* group. Long isolation and special adaptation to a relatively constant environment have led to less departure from the original ancestor of the group than is shown by the surface-forms, particularly *A. meridianus* itself, with the result that its characters have retained a more primitive form.

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ASELLUS CAVATICUS Schiödte. Male. $\times 14$.

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On the Morphology of the Larva of *Dorcus parallelopi pedus*, L. (Coleoptera).

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(With 7 Text-figures.)

[Read 14th February, 1929.]

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I. INTRODUCTION AND GENERAL FEATURES.

The present paper is intended as a contribution towards a more complete understanding of the morphology of characteristic types of Coleopterous larvæ. Access to abundant living material of the larva of the Lucanid beetle *Dorcus parallelopi pedus* afforded opportunity to make as complete a study as possible of its internal and external structure, which was carried out under the direction of Dr. A. D. Imms. Brief accounts of the external structure of the larva of *Dorcus* will be found in the works of Bree (1833), Ratzeburg (1837), Mulsant (1842), Dufour (1842), Perris (1877), and others, but the most complete description is that of Schiödt (1873). Since the work of the latter authority is over fifty years old, it is naturally somewhat out of date with respect to modern conceptions of morphology, and it makes no reference to internal structure.

The larva of *Dorcus parallelopi pedus* is of the typical Lucanid type, and is somewhat soft, fleshy, elongate in form, almost semicircular in section with flattened underside. It is usually bent in a curve and very often with the last three or four abdominal segments completely turned forward on the ventral side. The head is flexed downwards with its posterior edge covered by the fleshy anterior edge of the prothorax. Its colour is yellowish brown with

darker clypeus, labrum, and jet-black mandibles ; on its dorsal surface the Y-shaped epicranial suture appears whitish. There are no eyes. The body is divided into three thoracic and ten abdominal segments. When fully grown the larva is of large size, about 35 mm. long ; the sides nearly parallel from the prothorax to the eighth abdominal segment, whence it gradually tapers towards tip of abdomen. The maximum width occurs at the third or fourth abdominal segment, being about one-fourth the length of the body ; the maximum depth is at the eighth segment. The body is nearly pure white, deepening posteriorly to a dark grey or brownish tint, due to the dark colour of the viscera appearing through the transparent cuticle ; anteriorly on each side of the prothorax there is a narrow yellowish-brown chitinized plate which is dorso-ventrally directed. The thoracic segments are smaller than those of the abdomen, and each is provided with a pair of well-developed five-jointed legs. The abdominal segments are subequal in length dorsally, the first being the shortest and the penultimate one the longest. The cuticle of the first six abdominal segments is thickly beset dorsally with small denticles. The hindmost segment is somewhat conical in shape, and is provided on each side of the anal slit with a well-defined oval area.

II. EXTERNAL STRUCTURE.

(a) *Head.*

Head-capsule (fig. 1).—Semicircular with the anterior margin somewhat concave, narrower than prothorax ; its breadth related to the length about as $1.45 : 1$, widest at about third the length from base of antenna. Surface finely reticulate under high-power magnification. The number and arrangement of setæ as shown in fig. 1 is characteristic : in addition to these, numerous shorter setæ are present but are not constant in number and position, and for that reason have not been depicted in the figure. Occipital foramen in middle of ventral surface of head-capsule ; circular, slightly shorter in diameter than the length of head-capsule. The frons (F, fig. 1) is subtriangular, with a distinct dark median line extending forward from the posterior angle to about third its length ; wider than long, with maximum width related to maximum length as $3 : 2$, about two-thirds the length of head-capsule and widest anteriorly. Anterior margin is thickened and deeply pigmented at postero-lateral angles of clypeus.

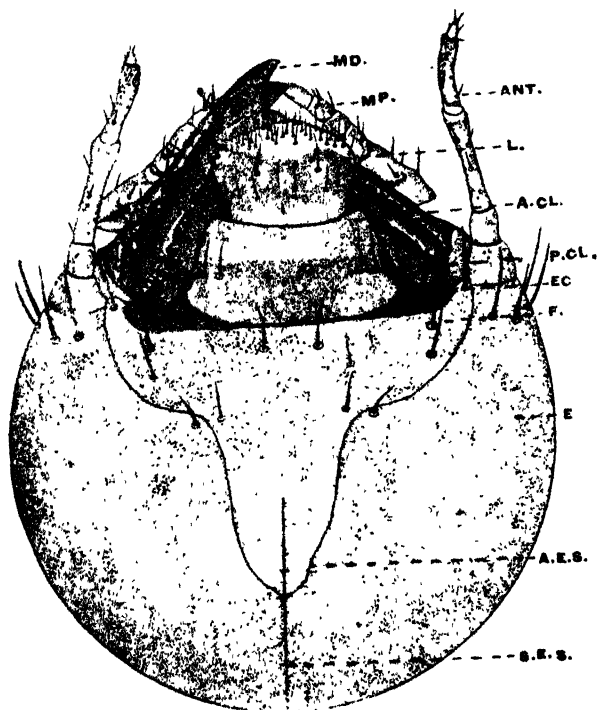
Epicranium (fig. 1, E.) divided posteriorly by the mid-epicranial suture (S.E.S.) and anteriorly separated from the frons by the arms of the epicranial suture (A.E.S.). The mid-epicranial suture about one-third the length of head-capsule and extending forward beyond the junction of the sutural arms into the frontal region. Corresponding with mid-epicranial suture is an internal ridge for muscle-attachments.

Clypeus (fig. 1) is well developed, trapezoidal, distinctly separated from frons, broad at base, the sides narrowed to the apical angles ; maximum length

related to maximum width about as 1 to 2.5. *Post-clypeus* (P.C.L.) more strongly chitinized and pigmented than ante-clypeus (A.C.L.); near anterior margin of post-clypeus there is a transverse lateral series of three setæ on each side, the outermost seta being much shorter than the other two.

Labrum (fig. 1, L.) is well developed, movable, sub-rectangular, with anterior margin convex and somewhat obtusely produced; anterior angles rounded, sides narrowing toward the base; total length a little longer than that of the whole clypeus; greatest length related to greatest width as 2 to 1.6. Dorsal

FIG. 1.

Dorsal aspect of head of larva, $\times 12$.

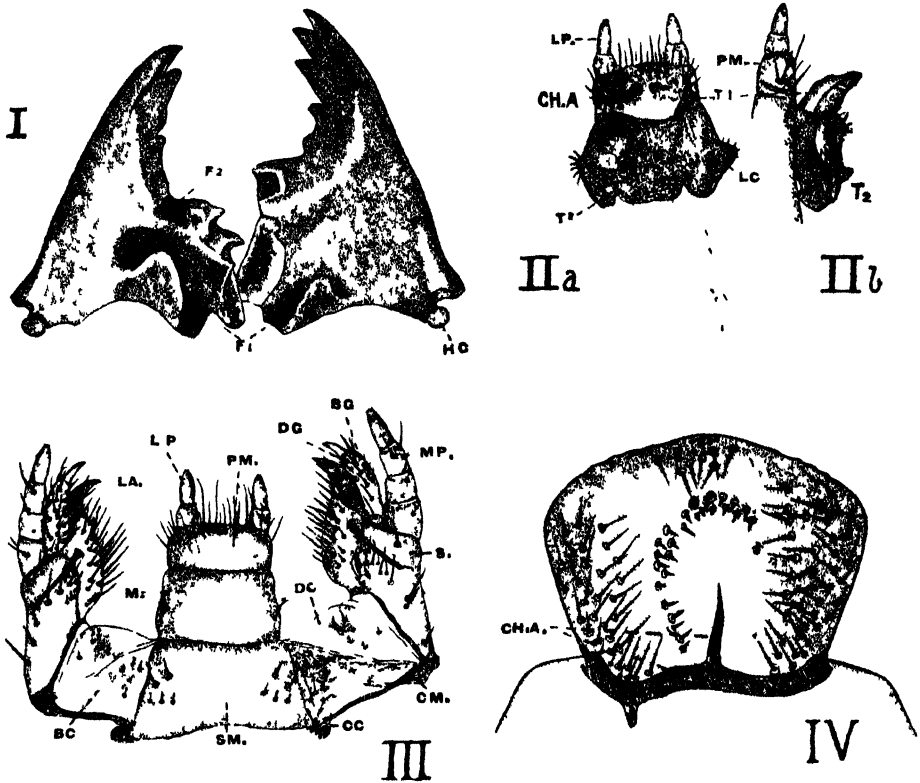
A.C.L., ante-clypeus; A.E.S., arms of epicranial suture; ANT., antenna; E., epicranium; EC., epicondyle of mandible; F., frons; L., labrum; MD., mandible; MP., maxillary palp; P.C.L., post-clypeus; S.E.S., median epicranial suture.

surface lighter-coloured anteriorly, where it is thickly beset with short stout setæ; a pair of long dorsal setæ and a variable number (about 7) of short posterior setæ are present.

Antenna (fig. 1, ANT.) well developed, almost as long as mandible, four-jointed, borne on a large conical basal membranous cone; basal joint cylindrical, about one-sixth the length of entire antenna; prebasal joint cylindrical, about

two and a half times the length of the basal joint ; subapical joint shorter than prebasal joint, being about four-fifths its length, slightly flattened laterally and produced anteriorly on its ventral side into a small accessory process of somewhat conical shape : apical joint small, about one-fourth the length of

FIG 2



Details of mouth-parts

I Mandibles, ventral aspect $\times 15$ IIa Labium and hypopharynx, dorsal aspect, and IIb Left ventro-lateral aspect of same, $\times 15$ III Maxillae and labium, ventral aspect, $\times 15$ IV Hypopharynx, $\times 32$

BC, basicardo, BG, basigalea, CC, condyle of cardo, CHA, chitinized area, CM, cardomarginal, DC, disticardo, DG, distigalea, F1, F2, fossae, HC, hypocondyle, LA, lacina, LC, lateral condyle, LP, labial palp, M, mentum, MP, maxillary palp, PM, prementum, S, stipes, T1, T2, dorsal and ventral teeth of hypopharyngeal sclerite

subapical joint, with its maximum diameter related to its length about as 1 to 1.5. All the joints with scattered conical rounded cup-like papillae, but the latter are more numerous on subapical joint where they nearly all bear

a minute stout seta. Basal joint anteriorly with a single seta; prebasal joint with about eight setae; subapical joint with three near base; apical joint with three near the middle and two at apex arising from a membranous area, the latter also with two or three peg-like projections or papillae.

The *Epipharynx* (fig. 2, IV) is membranous forming the under surface or palatal lining of the clypeus and labrum, merging posteriorly into the wall of the pharynx. It is strengthened by a narrow, strong, transverse band of chitin corresponding to or slightly behind the clypeo-labral suture; a median prolongation extends forward some distance from the transverse chitinized band (CH.A.). The sides of the epipharynx beneath the labrum are clothed with long stiff setae extending roughly in four irregular rows parallel with its lateral margin. In the middle region there is a shallow depression fringed on its right lateral border and anteriorly by a single row of stout, short, and somewhat blunt setae, which are inwardly directed; these setae are absent on the left margin. This asymmetrical arrangement of spines is probably associated with the structural differences of the two mandibles. Anteriorly the outer series is interrupted by two somewhat rounded, heavily chitinized, raised areas which appeared, in many larvae dissected, to be guarded in front by a group of about eight long stiff setae, near anterior margin of the epipharynx. On the surface of each area are two pit-like depressions. Immediately behind these chitinized areas are four very short, stout, peg-like setae arising from cup-shaped bases.

The *mandibles* (fig. 2, I) are strong and robust, with shiny black cutting and crushing edges. Each mandible is worked by two powerful muscles, an extensor attached to the dorso-lateral surface of the mandible and a retractor to the inner surface. The retractor is far the stronger of the two. Each mandible articulates ventrally with the hypostoma by means of a condyle (HC.) on its latero-ventral surface. Dorsally the mandible bears a condyle (fig. 1, EC.) which articulates with the frons close to the postero-lateral angles of the clypeus. Each mandible is about three-fourths the length of the head-capsule and bears a longitudinal series of three latero-dorsal setae (fig. 1, MD.). The general form of both mandibles is triangular, but their inner cutting-edges differ (fig. 2, I). On its inner surface the right mandible is produced into two and the left into three well-developed apical teeth; below the middle both carry a short blunt tooth; the left mandible also carries a small conical tubercle near the junction of the scissorial with the molar region; the latter regions of the right mandible are separated by a shallow groove or fossa (F_2) for articulation with the dorsal tooth of the hypopharyngeal sclerite (fig. 2, II, T_1). The molar region of each mandible bears ventrally a well-developed process bounding a fossa (fig. 2, I, F_1) which receives a corresponding process of the hypopharyngeal sclerite.

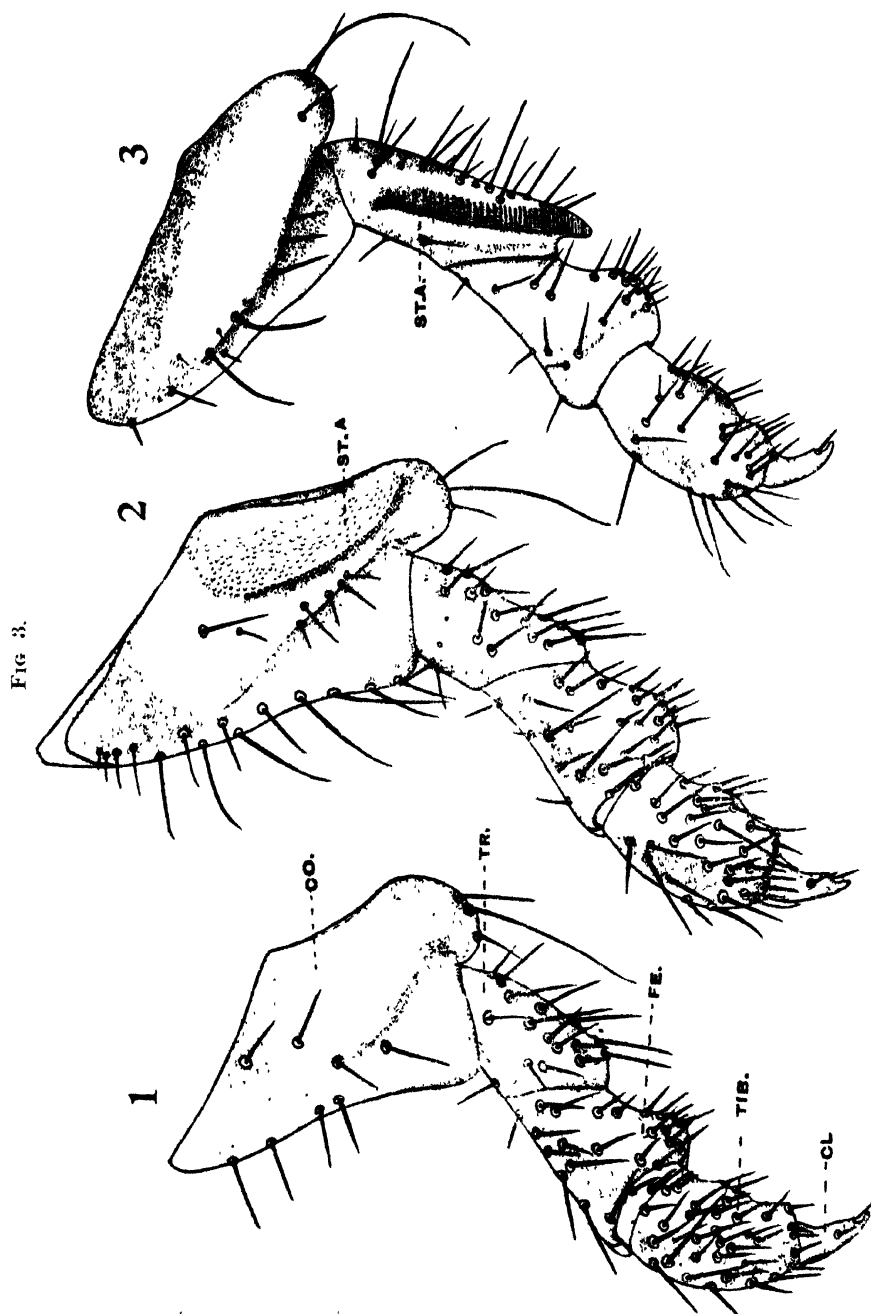
The *Maxillae* (fig. 2, III) are completely developed, with the full number of elements present. The maxillary palp (M.P.) is 4-jointed with the basal joint short and broad and about same length as the apical joint; prebasal joint

narrower, two-thirds the length of the basal joint, and bearing a rounded puncture below the middle on the ventral face; subapical joint about three-fourths the length of apical joint and on its ventral face, slightly anterior to inner border of lateral seta, are two rounded punctures; apical joint conical, about two and a half times longer than wide, with a few scattered punctures, finely papillose at the tip and with a very minute spine-like process near apex on inner border of ventral face. The *lacinia* (la.) is about the same length as the palpus—blade-like, armed with rows of strong setae on its inner border and distally produced into a strong chitinized tooth. The *galea* is somewhat lacinia-like in shape, divided into a large basal segment (BG.) and a distal claw-like projection (DG.) which probably correspond with *basigalea* and *distigalea* respectively of Crampton (1923). The galea is about three-fourths the length of palpi, with its basal segment armed with stiff setae and the distal claw half the length of the apical joint of the palpus.

The *cardo* is rather large, subquadrate, and separated distally from the stipes and proximally from the submentum by fine sutures. It is divided into two triangular sclerites, viz., a basal element (BC.) connected with the submentum and a distal element (DC.) connected with the stipes. Both areas are but slightly chitinized except for a narrow region (CM.) on the posterior border of the basal sclerite. These regions of the cardo are probably homologous respectively with the *basicardo*, *disticardo*, and *cardo-marginal* of Crampton (1923). The cardo articulates by means of a condyle (CC.) with the posterior angle of submentum. The *stipes* (S.) is about the same length, but narrower than the cardo, and is hinged to the latter. It overlaps the lacinia ventrally, and basally it is strengthened by a narrow, strongly chitinized, and pigmented region. Dorsally it is provided with an elongated tubercle, and one large seta slightly anterior to the latter. On the ventral side it is provided with setae as shown in fig. 2, III, S.

The *labium* (fig. 2, III) is composed of a well-defined submentum, mentum, prementum, and palpi. The *submentum* (SM.) is trapezoidal, broadest posteriorly, twice as wide as long and articulated laterally with the cardo. The *mentum* (M.) is smaller than the submentum, with its side-margins free, about one-third wider than long and bears the prementum on its anterior margin. The *prementum* (PM.) is transversely rectangular in shape, with the anterior angles rounded; its length in proportion to length of mentum as 3 is to 5; the anterior margin is almost straight and provided with closely-set large setae. The *labial palpi* (L.P.) are well developed and two-jointed; the proximal joint is thick and rounded, with few punctures; the distal joint more elongated and slender, about one and a half times the length of basal joint, twice as long as thick, with few scattered rounded punctures and several small papillae at its apex.

The *hypopharynx* is membranous and united with the pharyngeal surface of the labium. Beneath the mentum and distal margin of the submentum it is produced into strongly chitinized plate, or *hypopharyngeal sclerite*.



Legs, $\times 12.5$

1. Prothoracic, external lateral view. 2. Mesothoracic, external lateral view. 3. Metathoracic, internal lateral view.
CL., claw; CO., coxa; FE., femur; ST.A., stridulating area; TIB., tibio-tarsus; TR., trochanter.

The *hypopharyngeal sclerite* (fig. 2, II *a* and *b*) is an asymmetrical transverse structure. Dorsally it is produced into a strong buccal projecting tooth (T_1) which together with a shallow fossa on upper part of right mandible (fig. 2, I, F_1) forms a resistant surface against which upper portion of the molar area of the left mandible works. On either side the sclerite is produced into a somewhat conical projection (LC.) covered with short spines which articulates with hypopharyngeal fossa of the mandible (fig. 2, I, F_1). Dorsally the sclerite bears a blunt posterior tooth (T_2), and close to left extremity of the latter there is a fossa which receives the molar process on the buccal surface of the left mandible.

(b) *Thorax.*

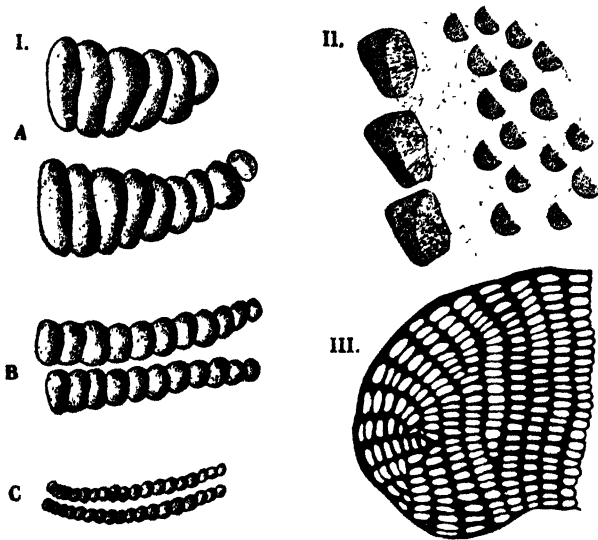
The prothorax is divided dorsally into two slightly raised areas by a transverse groove. Each area bears a transverse row of setæ. Laterally imbedded in the tergum above and in front of first spiracle is an elongated, dorso-ventrally directed, chitinous area. The mesothorax is also dorsally duplicated, the anterior area bearing a transverse row of setæ. The metathorax is simple (dorsally) and likewise carries a transverse row of setæ. A hypopleural chitination is present at base of legs on all the segments.

The *legs* (fig. 3) are 5-jointed, rather long and stout, with trochanter, femur, and tibia thickly beset with spine-like setæ. The *coxa* (CO.) is well developed, about twice as long as thick, with its proximal margin oblique; distally each coxa is produced into a rounded process which projects beyond the articulation with the trochanter on the inner side; coxa of second leg the longest and bearing a well-defined stridulatory area (fig. 3 (2), fig. 4 (II)) on its external posterior surface. The *trochanter* (TR.) large, about half as broad as coxa, with maximum length in proportion to breadth of pro- and meso-thoracic pairs nearly as 2 : 1 and of metathoracic pair about as 3 : 1; that of metathoracic leg provided on interior surface with a stridulating area (fig. 3 (3), S.T.; fig. 4 (1)). The *femur* (FE.) somewhat club-shaped, broadest distally, with maximum length related to maximum breadth as 3 : 2. The *tibio-tarsus* (TIB.) ovate, slightly constricted basally and almost as long as femur, but distinctly narrower. The *claw* (CL.) slightly curved and pointed, strongly chitinized and dark in colour, nearly half the length of tibio-tarsus, with a short but strong seta on inferior or concave side near apex; another and similar seta somewhat close to it on outer or posterior aspect.

(c) *Abdomen.*

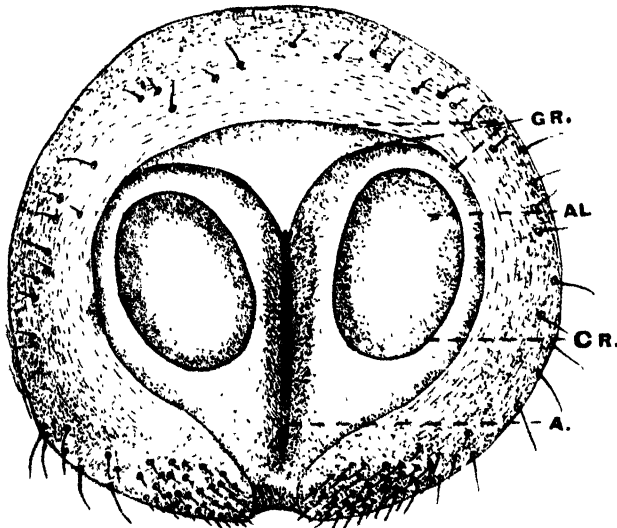
The first five abdominal segments are each divided dorsally into three areas: the median area is the most extensive and is provided with a transverse row of long fine setæ and is also thickly beset with small denticles, while the other areas are smooth and naked. The sixth segment is divided into two areas, viz.: (1) an anterior area with a transverse row of fine setæ and in front of these the cuticle is thickly set with denticles similar to those on the preceding segments, (2) a posterior area which is smooth and naked. The seventh to ninth segments

FIG. 4.



- I. Stridulating area on meta-trochanter.
 A. 6th and 7th rows from base. B. Middle region. C. 6th and 7th rows from base.
 × 341.
- II. Stridulating area on meso-coxa, × 341.
- III. Portion of mesothoracic spiracle, × 228.

FIG. 5.



- Tenth abdominal segment, posterior view.
 A., anus; AL., anal lobe; CR., chitinized ring; GR., groove. × 16.

are likewise each divided into two areas, viz., an anterior area bearing a row of long fine setæ and a narrow, smooth, naked posterior area.

The tenth abdominal segment (fig. 5) is much smaller than the ninth and is short and somewhat conical in shape. On its posterior surface it bears the anus (A.), which is a dorso-ventral slit. Embedded in the body-cuticle on each side of the anus is a chitinous ring (CR.) which encloses distinct well-defined anal lobes (A.L.). At the postero-ventral margin this segment is deeply emarginated, and the lip thus formed on each side is thickly beset with fine, inwardly-directed setæ.

(d) *Spiracles.*

Nine pairs of functional spiracles are present. They are located on the mesothorax and the first eight abdominal segments; a rudimentary spiracle can with suitable magnification be detected on the anterior margin of metathorax. The mesothoracic spiracle is located on a deeply seated lobe sunk into the posterior part of the prothorax, while the abdominal spiracles are placed anteriorly on their respective segments, except those on 7th and 8th segments, which are seated nearer the middle. They vary to a marked extent in shape and size. Each spiracle appears externally as a minute circular or oval area, surrounded by a broad, C-shaped, cribriform, chitinous respiratory plate and with the "C" directed obliquely cephalad and ventrad. In the last four spiracles the respiratory plate is much reduced and only slightly crescentic. The spiracle on the first abdominal segment is the largest, being about twice the size of those on 5th to 8th abdominal segments. The spiracle on the 6th abdominal segment is the smallest, being about half the size of that on the mesothorax. The perforations of the respiratory plates are comparatively large (fig. 4, III), almost oval in shape, and regularly distributed in more or less radial series.

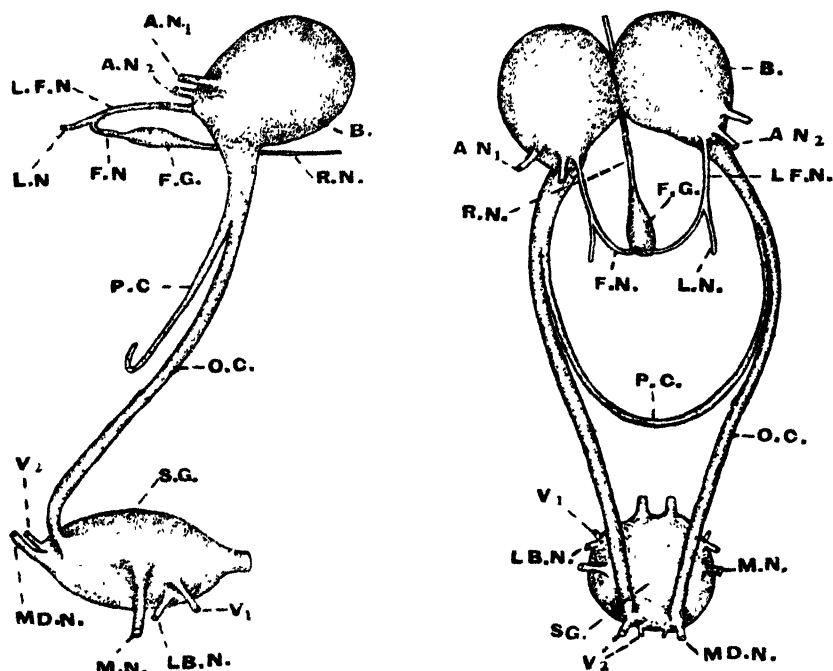
III. INTERNAL STRUCTURE.

(a) *Digestive System.*

Digestive System (fig. 7).—The alimentary canal extends as an almost straight tube from the front of the head-capsule to the last body-segment.

The *fore intestine* is short, extending back only as far as the middle of the mesothoracic segment, but, owing to the contraction and relaxation of the muscles of the head-capsule, the junction of the fore intestine and mid-intestine may be somewhat displaced from the normal position. Immediately behind the mouth the fore intestine dilates to form a *pharynx* from whose walls muscles radiate to the walls of the head-capsule. The pharynx quickly narrows to form a very short *œsophagus* (O.) of nearly uniform calibre: it is lined internally by a chitinous intima which is much folded longitudinally. Posteriorly, the *œsophagus* gradually expands into a thin-walled *crop* (CR.) which is also lined with chitin. Just where the fore intestine joins the mesenteron a very muscular constriction occurs which probably functions as an *œsophageal* or *cardiac valve*.

FIG. 6.

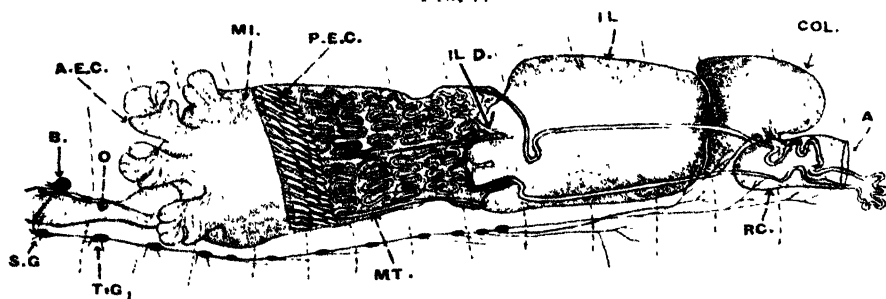


Supra- and sub-oesophageal ganglia. Left, lateral view. Right, frontal view.

× 40.

A.N.₁, antennary motor nerve; A.N.₂, antennary sensory nerve; B., brain; F.G., frontal ganglion; L.B.N., labial nerve; L.F.N., labro-frontal nerve; L.N., labral nerve; MD.N., mandibular nerve; M.N., maxillary nerve; O.C., para-oesophageal connectives; P.C., post-oesophageal commissure; R.N., recurrent nerve; S.G., sub-oesophageal ganglion; F.N., frontal nerve; V.₁, V.₂, 4th and 5th pairs of nerves.

FIG. 7.



Alimentary canal and central nervous system, lateral view, × 4.

(The fine broken lines indicate the limits of the segments.)

A., anus; A.E.C., anterior enteric coeca; B., brain; COL., colon; IL., ileum; ILD., diverticulum of ileum; MI., mid-intestine; MT., Malpighian tubes; O., oesophagus; P.E.C., posterior enteric coeca; RC., rectum; SG., sub-oesophageal ganglion; T.G.₁, first thoracic ganglion.

The *mid-intestine* (M.I.) forms the largest part of the digestive tract of this species. It passes as a straight tube from near the middle of mesothorax to the beginning of the 6th abdominal segment. It is broadest in front, gradually narrowing to the 4th abdominal segment, where a slight constriction is apparent; from here it again slightly dilates to meet the hind intestine. In large-sized larvæ it has a diameter anteriorly about two-thirds of that of the body and its posterior portion has a diameter of almost two-thirds that of the widest part. The most characteristic feature of the mid-intestine is the presence of an anterior and posterior series of short pouch-like enteric cæca. The *anterior enteric cæca* (A.E.C.) are eight in number, four on each side; two are latero-dorsally placed, one behind the other, while the other two are situated laterally and latero-ventrally, respectively. Each cæcum is lobulated, and it differs histologically from the remainder of the mesenteron. Internally each lobe is much folded and the folds themselves are composed of very elongated narrow cells. The *posterior enteric cæca* (P.E.C.) are about 100 to 120 in number, 50 to 60 on each side, and are arranged in a band of three rows which presents a somewhat U-shaped appearance with the arms dorsally directed and almost meeting at the mid-dorsal line. The cæca of the hindmost row are the longest, while those of the middle row are intermediate in this respect. Furthermore, the cæca in each series gradually increase in size from the dorsal towards the ventral side.

The *hind intestine* consists of three regions—ileum (IL.), colon (COL.), and rectum (RC.). The *ileum* occupies the greater part of the body-cavity from the beginning of the 6th to the rear part of the 8th abdominal segment. It has the form of a straight tapering tube whose posterior diameter is about two-thirds that of the anterior end. At its juncture with the mesenteron in front there is a well-marked constriction which possibly functions as a *pyloric valve*. From the anterior margin of the ileum there arise five short lobular diverticula, which are appressed to the walls of the posterior end of the mid-intestine. Four of these diverticula lie laterally, two on each side, while the other is seated ventrally. The dorso-lateral diverticulum is unilobed and shorter than the others. The ventro-lateral diverticulum is bilobed and slightly longer than the ventral diverticulum. The latter is trilobed, the median lobe being extremely short and blunt. The *colon* which follows is separated from the ileum in front and the rectum behind by distinct constrictions. Its shape and size vary enormously with the amount of residual products of digestion present. Generally it occupies the greater part of the body-cavity of the 9th and 10th abdominal segment. Anteriorly it is usually concave where it is applied to the hind end of the ileum. From this point it overlies the rectum and forms with the latter a somewhat **S**-shaped bend. The *rectum* is pyriform in shape, with the narrower end posteriorly directed. It is very muscular, and there are also strong bands of muscle-fibres which originate on the external surface of the rectum and are inserted into the body-wall. Finally, the rectum opens to the exterior through the anus (A.), which is a simple dorso-ventral slit situated in a groove in the centre of the 10th abdominal segment.

The *Malpighian tubes* (fig. 7, M.T.) are simple, long, thread-like tubes of uniform diameter throughout, closely appressed to the walls of the mesenteron in front and to the rectum behind. They open at their proximal extremities into the alimentary tract at the juncture of the mesenteron and the hind intestine. There are four of these vessels, two on each side, whose points of origin are latero-dorsal and latero-ventral, respectively. At their apices the tubes of each side are confluent, thus presenting the appearance of loops.

The dorsal tube at first runs ventrally, passing beneath the dorso-lateral diverticulum of the hind intestine, and then proceeds forward along the mid-lateral line of the mesenteron to a point close to the posterior enteric cæca. From here it curves dorsally and pursues a winding course, being thrown into numerous folds and loops on the dorso-lateral surface of the mesenteron from the region of the posterior enteric cæcæ to the anterior margin of the hind intestine. It then continues posteriorly almost in a direct course along the side of the hind intestine on to the dorsal surface of the rectum. Here it becomes convoluted before passing to the oval areas at the tail end of the body, where it is thrown into several folds which are closely applied to the external cuticle of the body-wall.

The ventral tube (M.T.) arises between the ventro-lateral and ventral diverticula of the hind intestine, and passes forwards in an almost direct course close and parallel to the mid-ventral line of the mesenteron. At a point near the posterior enteric cæca it curves dorsally and forms very numerous convolutions which almost completely cover the ventro-lateral surface of the mesenteron. The tube then continues posteriorly, following near the mid-ventral line of the ileum. From here it takes a direct course and becomes continuous with the dorsal tube at the hind end of the body.

(b) *Nervous System.*

The general features of the nervous system of *Dorcus* larva indicate on the whole, a conformity to the simple type found in many insect-larvæ. It may be conveniently divided into the brain, the ventral nerve-cord, and the visceral (or stomatogastric) system.

Brain (fig. 6, B.).—The brain is two-lobed and lies in the upper part of the head-capsule directly below the rear half of the frons. Each lobe is somewhat ovoid in shape with the narrow end directed obliquely forward and downward. Three nerves arise from the antero-dorsal surface of each lobe. The outer and most posterior one (A.N₁) takes a lateral course and innervates the muscle-fibres near base of antenna, and is therefore probably a motor nerve. The median nerve (A.N₂) runs almost parallel with, and in front of, the outer nerve and enters the cavity of the antenna. The root of the remaining nerve, the *labro-frontal nerve* (L.F.N.), lies close and to the inside of the median. Near the posterior margin of the labrum it divides into a *frontal nerve* (F.N.), which unites with the *frontal ganglion* (F.G.), and the *labral nerve* (L.N.). The latter passes forward along the lateral region of clypeus and finally enters the labrum.

The *subœsophageal ganglion* (S.G.) is somewhat oval in shape and is situated slightly anterior to the brain. It lies between the hypopharynx and the labium, immediately behind the posterior margin of hypopharyngeal sclerite and above the anterior border of submentum. The *para-œsophageal commissures* (O.C.) are thick bands which arise from the underside of the anterior extremity of the brain and unite with the upper surface of the anterior end of the sub-œsophageal ganglion. The *post-œsophageal commissure* (P.C.) is a relatively thin strand of nerve-fibres which forms a loop below the œsophagus immediately in front of the para-œsophageal commissures, and is joined with the latter dorsally. The sub-œsophageal ganglion gives rise to five pairs of nerves, as follows :—

(a) The *mandibular nerves* (MD.N.) which arise just below and slightly in front of the insertion of the para-œsophageal commissures (O.C.). Each passes to the base of the mandible, where it divides into branches innervating this appendage.

(b) The *maxillary nerves* (M.N.) arise from the dorso-lateral face of the ganglion about midway along its length. Each nerve passes into the cardo, giving off branches which are distributed to the musculature of this sclerite, and continuing onward enters the stipes where it gives rise to several fine branches.

(c) The *labial nerves* (LB.N.) arise from the latero-ventral face of the subœsophageal ganglion about two-thirds its length from anterior end. Each of these nerves passes to the apex of the labium, dividing along its course into several branches.

(d) The *fourth pair of nerves* (V_1) arises from the lateral surface of the ganglion about third its length from the posterior end. These nerves are very slender and correspondingly difficult to trace. They pursue a caudal course, turning slightly ventrad and laterad, to the posterior region of the submentum. Here each divides into two branches, the course of which has not been followed.

(e) The *fifth pair of nerves* (V_2) are also short and extremely slender. These arise from the anterior face of the subœsophageal ganglion. Their point of origin is to the inside of the mandibular nerves, directly below the inner borders of the para-œsophageal commissures. Each of these nerves passes to the latero-posterior margin of the hypopharyngeal sclerite, where it divides into several extremely fine branches.

The *Ventral Nerve-cord* (fig. 7) consists of 11 ganglia united by separate connectives. In the thorax the three ganglia (T.G.) show no sign of fusion and each lies in its respective segment. There are eight abdominal ganglia, the first lying just within the third thoracic segment; the second abdominal ganglion thus comes to lie inside the first abdominal segment, and, in this way, each of the first five abdominal ganglia is displaced and is situated in the segment in front of the one to which it actually belongs. The sixth abdominal ganglion

lies just within the fourth abdominal segment and the 7th and 8th are situated close together in the fifth segment. The eighth abdominal ganglion is slightly larger than the others and probably represents a fusion of the last three abdominal ganglia.

Each thoracic ganglion gives off two pairs of lateral nerves. The first pair arises from the connectives close to the points where the latter join their respective ganglia anteriorly. These nerves give off branches to the ventral and lateral body-musculature, and ultimately break up into several branches on the latero-dorsal aspect of the body. The mesothoracic pair also gives off an ascending branch which supplies the spiracle.

The second pair of nerves is much stouter and takes origin from the middle of the lateral margins of the ganglion. Each nerve gives off two main branches which innervate the muscles at the base of the coxa, and finally enter the cavity of the coxa itself.

Each of the abdominal ganglia, exclusive of the last ganglion, possesses but one pair of lateral nerves. Each of these arises from the postero-lateral margin of the ganglion close to the point where the latter joins the connective. Each nerve runs posteriorly, almost parallel to the main nerve-cord, into its respective segment and then passes laterally, giving off branches along its whole length to the musculature of the body-wall. It finally passes to the muscles on the latero-dorsal surface of the body.

The 8th abdominal or terminal ganglion gives off two pairs of nerves. The first pair arises from the lateral margins of the ganglion little behind the middle. Each nerve runs posteriorly into the 8th abdominal segment and, after giving off a branch to the ventral trunk-muscles and another to the viscera, passes to the latero-dorsal trunk-muscles.

The second of the two pairs of nerves given off is much stouter and arises from the posterior margin of the ganglion. Each nerve passes posteriorly, giving off a branch which divides into smaller branches supplying the viscera and muscles of the 9th abdominal segment: it then continues backward and becomes sub-divided into several branches innervating the viscera and muscles of 10th abdominal segment.

The Visceral Nervous System.—The visceral or sympathetic nervous system consists of the *frontal ganglion* and the nerves associated with it. The frontal ganglion (fig. 6, F.G.) is pyriform in shape and is situated above the oesophagus, a short distance in front of the brain. It is connected with the latter by means of the *frontal nerves* (F.N.) which arise from the ganglion at its anterior extremity. From this point they curve gradually posteriorly to join with the roots of the labral nerves (L.N.) as already described. Posteriorly the frontal ganglion gives off a *recurrent nerve* (R.N.) which runs in close contact with the dorsal line of the alimentary tract and, passing beneath the brain, expands a short distance behind the latter centre into a *hypocerebral ganglion*. The recurrent nerve leaves the hypocerebral ganglion and immediately divides into two branches. Each branch passes obliquely backwards and ventrally and becomes lost to sight among the muscles of the posterior margin of the fore intestine.

IV. CONCLUDING REMARKS.

In the foregoing description the detailed external morphology of the larva of *Dorcus* is described, together with the salient features exhibited by the digestive and nervous systems.

Apart from other characters the larva of *Dorcus* can be separated from those of other European genera of Lucanidæ by the form and arrangement of the tubercles composing the coxæ and trochanteric stridulatory areas.

In its internal anatomy it exhibits affinities with certain genera of Scarabæidæ in the presence of three series of cœca or diverticula of the alimentary canal. The great lateral pouch-like cœcum of the colon, described in *Cetonia* and in the Coprinæ, is represented in *Dorcus* by a general dilatation of that region of the gut, rather than by a lateral diverticulum. The Malpighian tubes were found to differ considerably from the early account given by Dufour (1842), in that the two tubes of a side form a complex loop, owing to their distal extremities being confluent instead of terminating independently as described by that observer. This condition is rare among insects, but is described by Bugnion (1920) in the Lampyridæ.

The nervous system is of an exceptionally primitive character as in *Lucanus*, and does not exhibit the great concentration of the ganglia of the ventral nerve-cord prevalent in larvæ of the allied family Scarabæidæ.

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The Anatomy and the Histology of Bud-formation in the Serpulid *Filograna implexa*, together with some Cytological Observations on the Nuclei of the Neoblasts*. By G. H. FAULKNER, Demonstrator in Zoology in Bedford College, University of London. (Communicated by Dr. W. T. CALMAN, F.R.S., F.L.S.)

(PLATES 7 & 8, and 33 Text-figures.)

[Read 31st January, 1929.]

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INTRODUCTION.

Most of the material for this paper has been collected, and much of the work performed, at the Marine Biological Laboratory, Plymouth. The author wishes to thank Dr. E. J. Allen, F.R.S., Director of the Laboratory, for his constant assistance, and also to thank Professor J. H. Ashworth, F.R.S., for reading and criticising the manuscript.

There are several reasons why the genus *Filograna* is particularly suitable for morphological investigation. In the first place, there is no very complete account of any Serpulid in the literature, and, secondly, this is a British form which is both abundant and easily obtainable; further, its small size makes it

* This paper formed the main part of a thesis approved by the University of Edinburgh for the degree of D.Sc., January 1929.

easy to manipulate. Then, also, it offers two points of special interest in connection with its reproductive habits. It is hermaphrodite, and it reproduces asexually by means of posterior terminal buds. This is a rare phenomenon among Polychæta outside the family of the Syllidæ. Budding in one individual *Eulalia* is recorded by Verrill (1873), and in *Myxicola* and *Potamilla* among Cryptocephala by Caullery and Mesnil (1920).

The budding in Syllids is a feature of the same nature as epigamy, *i. e.*, the completion of a bud marks the time of sexual maturity, and the division between bud and stock coincides more or less accurately with the division between sexual and asexual zones of the body. In *Filograna* the relationship between bud and stock is somewhat inconstant. The budding individual generally shows no sexual organs; in cases in which these are visible, they are confined to the stock (or parent individual); also, when a bud is formed on a stock containing sexual organs, these are never so abundant as they are in a mature non-budding individual. The sexual and asexual phases appear to be entirely independent of each other, and may overlap, or may follow in sequence. The conditions, in fact, are more similar to those seen in *Oligochaetes* than to those in other Polychætes, and the two possible arrangements in the case of *Filograna* may even be compared with parallel cases in separate genera of *Oligochaetes*: in *Ophidonais*, the sexual and asexual processes are mutually exclusive, while in such genera as *Nais* and *Chaetogaster* the two overlap more or less. A similar comparison is seen when the position of origin of the bud on the parent individual is considered (see p. 128). Probably the habit of budding has been developed in this genus simply as an adaptation to sedentary life.

The most recent and most complete general account of the genus *Filograna* is that of McIntosh (1923), in whose monograph a full historical survey and bibliography of the genus are given, together with details of the distribution, the form of the colony, and of the chaetæ.

There is one point brought forward by McIntosh which may be mentioned, and that is his decision regarding the classification of the two species *Filograna implexa* Berkeley and *Salmacina dysteri* (Claparède). I agree with McIntosh that there is insufficient reason to justify the separation of these into two genera. The chief difference between them lies in the fact that *Filograna* has its dorsal-most branchiæ modified to form opercula and *Salmacina* has not.

Both occur in the Plymouth area and both were examined in large numbers. Material obtained from the town pier is of the typical non-operculate type, and that obtained from deeper water on the Mewstone ground operculate. But other samples taken inside the Sound, on Winter Shoal and the G.W.R. Docks, contain both varieties.

There are also other differences, apart from opercula, found when samples from several collecting-grounds are compared. For instance, the "*Salmacina*" colonies on the pier are bright red in colour, as are those found in deep water at Revelstoke Point, while those on the other grounds mentioned (producing pure "*Filograna*" or the mixed colonies) are brownish, as a result of the

absence of the red pigment. The presence or absence of pigment has no relation to the depth at which the animals are growing. These collections have all been made between low water and a depth of about 15 fathoms, a comparatively small range.

A second feature, which is variable, is the size of the thorax. The number of thoracic segments varies among the individuals of one colony within a range of about four segments (round a normal of seven).

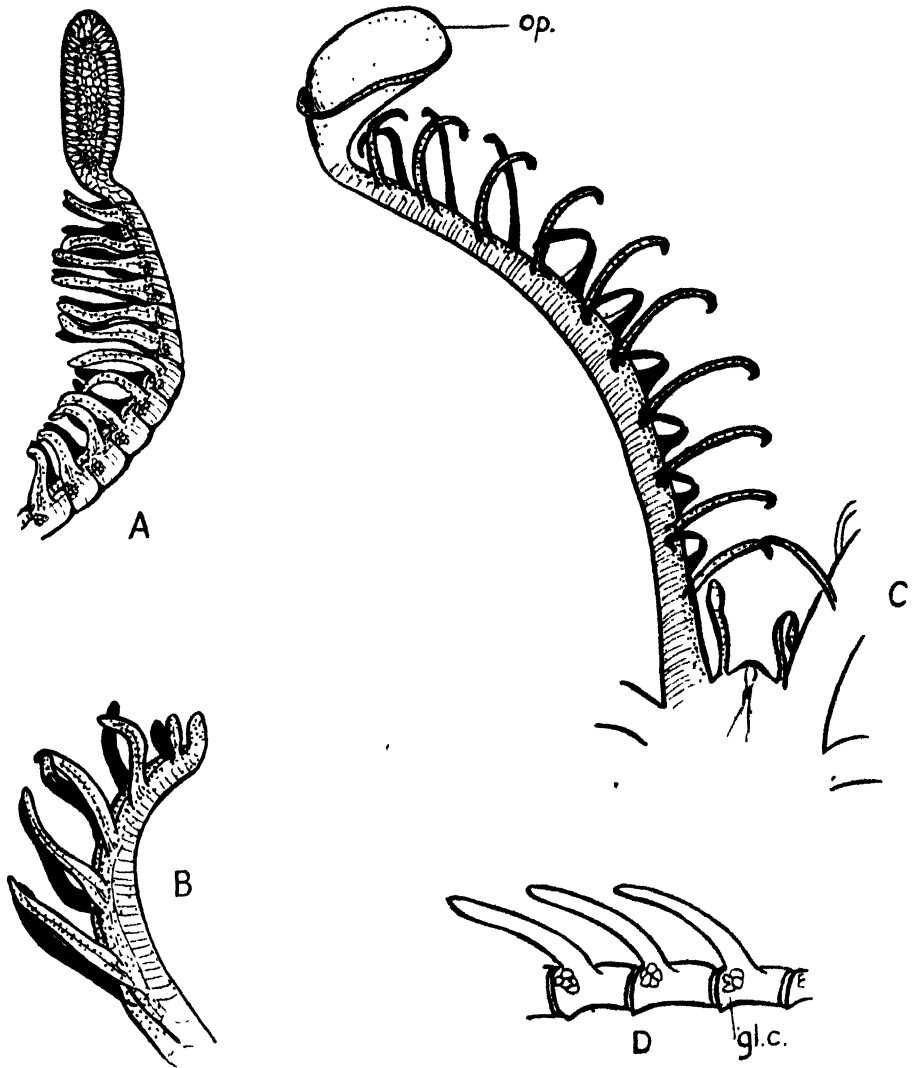
Thirdly, the form of the colony varies: in one case there are encrusting groups of tubes, and in another large fenestrated masses 10 or 15 cm. in diameter. Between these two extremes are gradations, not due to the age of the colony, but characteristic of the area and of the substratum to which the tubes are attached. The non-operculate "*Salmacina*" forms massive clumps attached to rocks, the operculate form on the Mewstone is always found encrusting on *Lepralia*, and the mixed colonies are usually intermediate in size and attached to—or embedded in—sponges and other sedentary animals.

One fact which may help to account for the small size of the Mewstone colonies is that a certain Monstrillid parasite, *Hamocera*, is abundant here (for life-history of *Hamocera*, see Malaquin, 1901). Many of these tubes when broken are found to be empty, so it may be that the parasite diminishes the vigour of the colonies and prevents them from attaining a greater size. The reason why the parasite is restricted to one locality is not known. It may be a geographical one, but even if it is physiological and taken as evidence of specific difference it still does not seem to justify the two genera.

Further, to return to the account of variation in the species, there are several ways in which the branchiae themselves may be modified, and the presence of an operculum on the end of a filament does not seem to be any more significant than the presence of any other particular kind of termination. The number of pinnules may vary between 12 and 24, and these may be all more or less equal, or may diminish in size distally. Also, some filaments possess a rounded opaque swelling at the base of each pinnule, while others, on the other hand, have similar glandular cells forming a row up the outer face of the whole axis. The termination of the filament (see text-fig. 1) is sometimes a small rounded tip, smaller than the smallest and most distal pinnule, and sometimes is enlarged and opaque, swollen with glandular cells. The enlargement of the tip may be confined to the two dorsal filaments only, or it may apply to all the eight equally. Two extremes of these conditions of size are as strikingly different as an operculate and a non-operculate filament ever are. It is not suggested that the opercula have any function other than that of closing more effectively the mouth of the tube, and if such a character be made of generic importance it is of an entirely different order of magnitude from that of the differences which separate the other genera of Serpulids.

The presence or absence of opercula does not seem to show any correlation with the variation of other organs; these data are therefore interpreted as supporting the conclusion reached above that the two forms *Filograna implexa*

TEXT-FIG. 1.



Branchial filaments of four individuals, showing variations of form.

- A Filament with enlarged glandular termination. B. Terminal portion of filament without glandular enlargement. C. Dorsal filament with operculum. D. Three pinnules, with the group of glandular cells at their base.

gl.c., glandular cells; *op.*, operculum.

and *Salmacina dysteri* are synonyms, and the former is retained. This classification does not agree with that of Fauvel (1927) in his most recent monograph.

EXTERNAL FEATURES.

1. General.

When the worm is in its tube and expanded, a circle of colourless branchiæ, the bright red head, and two or three anterior somites are protruded from the opening, but on the slightest stimulation the whole is rapidly withdrawn.

The body measures between 1 mm. and 4 mm. in length and has an average diameter of 0.3 mm. At the anterior end of the body is a branchial funnel, formed of eight pinnate filaments, commonly 0.8 mm. to 1.0 mm. in length, but in a particularly handsome variety obtained from Revelstoke Point they attain a length of 1.8 mm., *i. e.*, the same length as the rest of the animal. In a sample taken at Naples they even exceeded the length of the rest of the animal considerably. The body itself is divisible into three zones. Anteriorly is the thorax, which contains generally eight or nine segments, though any number between five and eleven occurs in the adult. The thoracic segments are larger than the abdominal, the actual size being variable. Sometimes a thorax is equal in length to an abdominal region of twice the number of somites: such a conspicuously long thorax may measure 1.5 mm. The length of the abdomen depends upon age and maturity: it may contain as few as six, or as many as forty segments. There is an intermediate zone consisting of two segments which have lost their parapodia, and this is referred to as the achæitous zone. Posteriorly the body terminates in two lobes—the anal papillæ.

There are structural details in which the thorax and abdomen differ, concerning colour, presence of a membranous outgrowth, form of parapodia, and distribution of cilia.

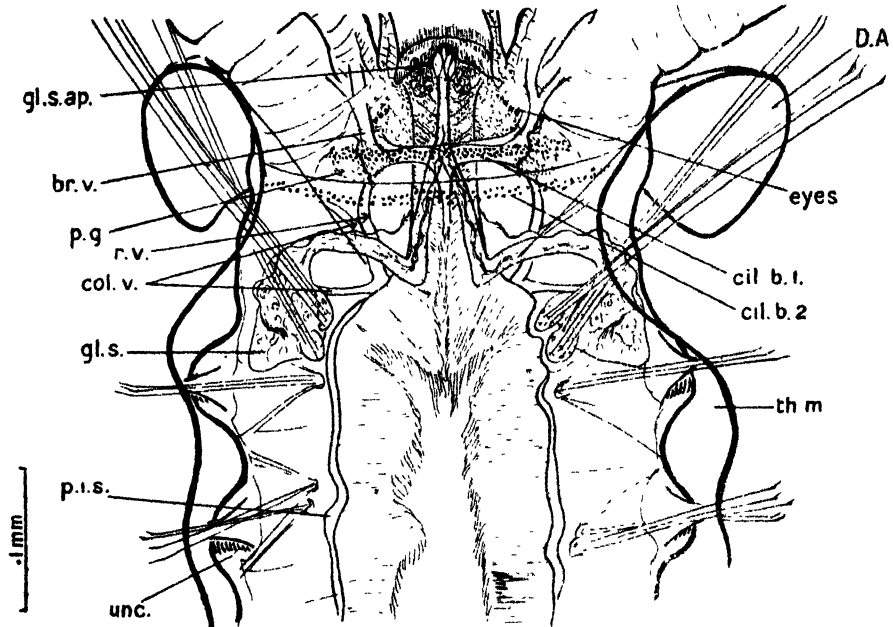
The red colour which tinges the colony is almost entirely confined to the thorax, particularly to that part which is protruded from the tube when the animal is expanded. Further, the dark brown colour of the anterior gut is seen through the walls of the thorax. The abdomen is comparatively pale and clear, and owes what colour it has to the presence of granules in the gut, to blood in the sinuses, and to the genital organs.

The thorax bears a membranous outgrowth, the thoracic membrane, which has the form of two longitudinal folds, one on each side dorsal to the parapodia. They are united posteriorly by a small transverse ventral fold and anteriorly by another such fold, immediately behind the branchiæ. This latter, the collar, is enlarged, particularly at the angles where the lateral and ventral parts are confluent. The collar is inserted pointing forwards and has this position when the animal is in its tube, but is rolled back over the aperture of the tube when expanded. The thoracic membrane points obliquely outwards and upwards when out of the tube, but when withdrawn the two halves overlap and form a tubular supra-thoracic canal (see text-fig. 3). This membrane arises in the

position of, and is probably homologous with, the dorsal cirrus of other Polychætes. The collar is merely the enlarged anterior end of the membrane, the two halves of which have grown round the sides of the first segment and have fused ventrally.

The membrane is supported by the long chætæ of the thorax, arising in the dorsal lobe of the parapodium: in the ventral lobe is a row of hooked uncini. In the abdomen the arrangement is reversed, the long chætæ being ventral and the uncini dorsal. The lobes bearing the long chætæ in the case of the thorax are long and slender, merely an investment of the base of the bristles:

TEXT-FIG. 2.



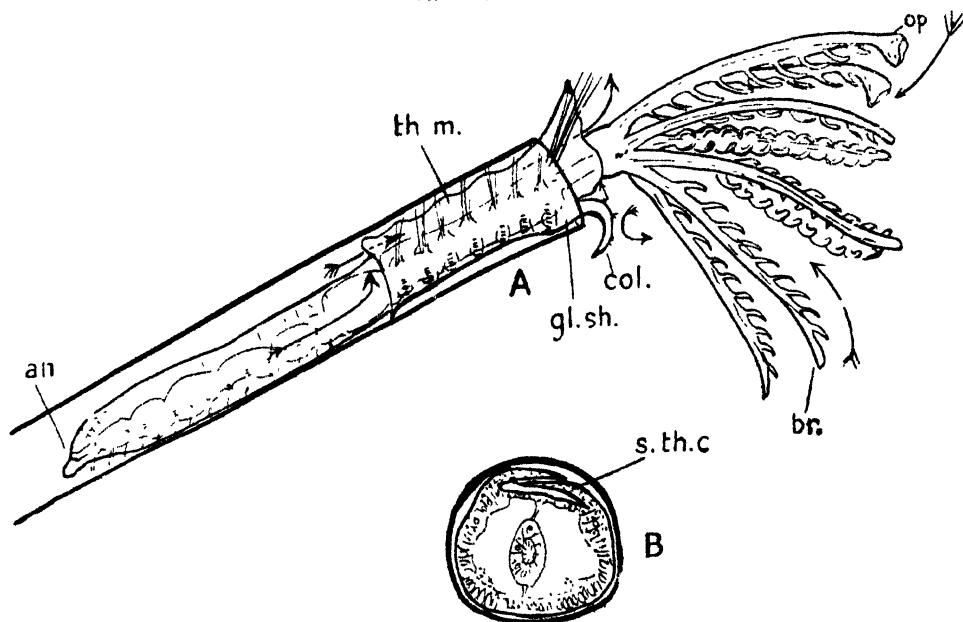
Semi-diagrammatic view of anterior end as seen from the dorsal surface.

br.v., branchial vessel; *cil b. 1.*, first transverse ciliated band; *cil. b. 2.*, second ditto; *col. r.*, blood-vessel of collar; *D.A.*, dorsal angle of collar; *gl.s.ap.*, aperture of glandular sac; *gl.s.*, glandular sac; *p.g.*, posterior cerebral ganglion; *p.i.s.*, peri-enteric sinus; *r.v.*, ring-vessel; *th.m.*, thoracic membrane; *unc.*, uncinus.

the ventral lobe has the form of a thick transverse ridge in which the uncini are embedded. In the abdomen the neuropodium is smaller, and the notopodium has almost vanished. In the anterior abdominal segments there is another lateral finger-shaped outgrowth immediately behind the uncinal lobe of the parapodium: this forms a tubular canal, the coelomoduct, and when the segments are filled with the maturing sexual cells, these tubes enlarge, acquire an opening to the exterior, and act as the genital ducts: as mentioned below, they become ciliated at this time. Behind the genital somites these tubes diminish in size, and at the extreme hind end are entirely absent.

The long chætæ are of two patterns : one has tapering capillary shafts and the other has flattened toothed blades near the tip (described and figured by M'Intosh, 1923). The first bundle contains both kinds, a group of four to six capillaries, and another group containing about the same number of the complex type. The average length of these is 0.3 mm. There are no uncini on this somite, but its long chætæ are the longest in the body : they support the enlarged angles of the collar. The following somite has both long chætæ and uncini, but in this case the long ones are all capillaries and in one bundle, numbering about six. This segment bears a row of 20 to 30 uncini, inserted with their teeth pointing

TEXT-FIG. 3.



A. The animal in its tube, with the branchiae expanded; the arrows indicate the direction of the ciliary currents. B. Transverse section through the thoracic region of the animal in its tube.

an., anus; *br.*, branchiae; *col.*, collar; *gl. sh.*, gland-shield; *op.*, operculum; *s. th. c.*, supra-thoracic canal (the indication line should extend into the clear space); *th. m.*, thoracic membrane.

forwards and the small hooks backwards. All the following thoracic somites are provided with both kinds of long chætæ and uncini. They have a group of three to five of the simple form and another of two or three complex, all measuring about 0.2 mm. In the abdominal segments the long chætæ are reduced to one or two per parapodium, and have a length of 0.12 mm. only. Similarly, the uncini are reduced in number also, five per segment being the average in the abdomen.

The intermediate achæitous zone is derived from the two anterior abdominal segments by the loss of their appendages. Firstly the chætæ disappear, then the parapodial lobes and coelomoducts.

There is a difference in the arrangement of cilia on the anterior and posterior segments. On the abdomen the ventral surface is ciliated, the ciliated cells being scattered evenly along it and accurately confined to that area of the epidermis which lies beneath and between the two ventral nerve-cords. In addition, there are tufts on the anterior faces of the notopodia, close to the openings of the coelomoducts. On the thorax cilia occur on the dorsal surface only, on the body-wall between the insertion of the two halves of the membrane and on the dorsal surface of the membrane itself. In the achæitous zone, the intermediate lateral walls are ciliated, viz., the area between the nerve-cords and the dorso-lateral lines; hence there is a ciliated band parallel to, and just posterior to, the hind margin of the thoracic membrane. The significance of this in connection with the course of the ciliary currents is demonstrated later (p. 118).

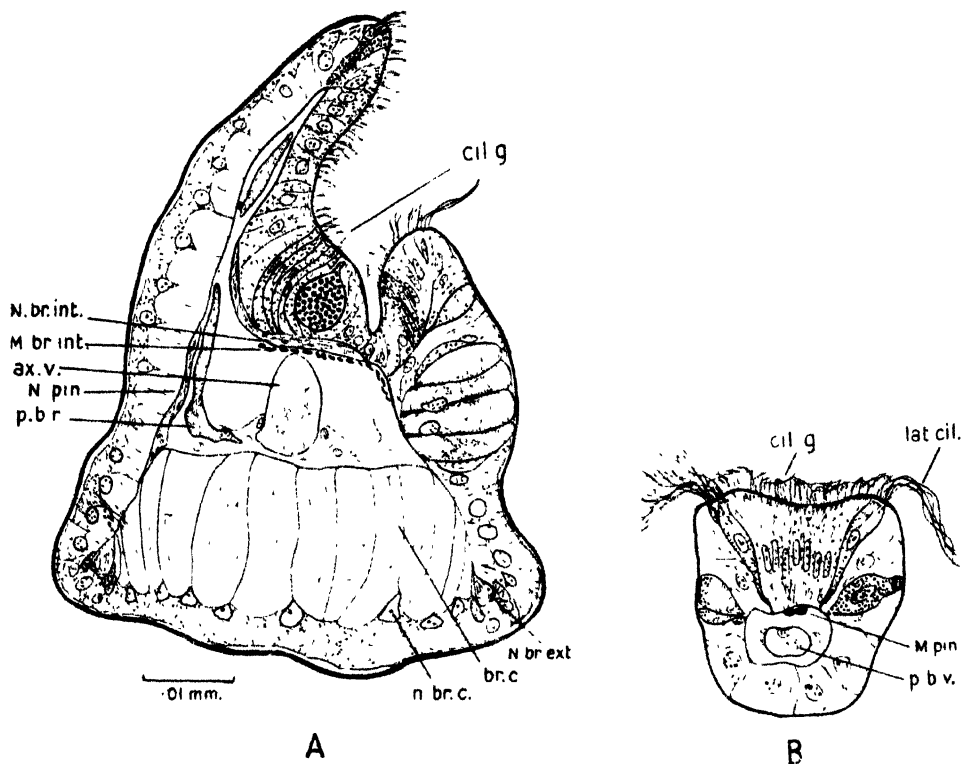
Anterior to the segmented part of the body is the prostomium, projecting in front of the collar as a rounded lobe and terminating in a small median papilla (text-fig. 22). This papilla is ciliated dorsally, and bears at its tip the opening of the duct of the glandular sac. The head carries the eyes, two oblique rows of dark masses which sometimes appear structureless and sometimes as distinctly cup-shaped. In the larva, when there is a single pair only, the fact that the pigment is really arranged round a hollow cup is most clearly seen; in the adult there is on each side a row of about six (text-fig. 21).

Ventral to the head is the proboscis, a long non-retractile tube, terminating in a slightly funnel-shaped opening (the mouth) and extending a little anterior to the tip of the head. It is separated from the head by a deep groove, which is closed laterally by the semicircular base of the branchiæ. The common branchial base is united with the sides of the head dorsally and with the proboscis ventrally, and in both cases the line of junction is perfectly distinct and sharply defined, although it is not a habit of this animal to break off its branchiæ autotomously. The junctions dorsally are two oblique lines as in text-fig. 2, and ventrally are two lines parallel to these, reaching towards the middle line as far as the longitudinal proboscis-muscles. Posteriorly they reach almost as far as the insertion of the collar. The clearness of the division is due to the fact that the head is strongly pigmented, while the branchial base is formed of clear transparent cells.

Division into four filaments on each side occurs at the level of the tip of the proboscis; each filament is provided with two rows of lateral branches, the pinnules, arranged alternately. Arising at the angles of the head, between the bases of the dorsalmost filaments, is a pair of ciliated finger-shaped tentacles, overhanging the mouth-opening. Between the bases of the pinnules, along the sides of the filaments, are patches of opaque cells swollen with globules (text-fig. 1); in some cases these are scattered evenly along the external face of the filament. When stained with Mayer's muci-carmin, these cells show a pale pink colour.

The termination of the main axis, *i. e.*, the region distal to the last pinnule, sometimes is merely a small rounded tip and sometimes is thickened and greatly elongated (text-fig. 1); one example measured 0.5 mm. on a filament of total length 2 mm. These swollen tips are packed with a mass of opaque cells similar to those just mentioned. In other cases the two dorsal filaments have their tips modified to form opercula. In the development of these the end of the axis becomes flattened, then the edges are rolled back and fused together, so that a cup-shaped structure results.

TEXT-FIG. 4.



A. Transverse section branchial filament B. Transverse section branchial pinnule.
ax.v., axial vessel; *br.c.*, cells of branchial axis; *cil.g.*, ciliated groove; *M.br.int.*, internal branchial muscle; *M.pin.*, internal muscle of pinnule; *lat.cil.*, long lateral cilia; *N.br.ext.*, external branchial nerve; *N.br.int.*, internal branchial nerve; *N.pin.*, nerve to pinnule; *n.br.c.*, nuclei of axis-cells; *p.b.v.* & *p.b.r.*, blood-vessel of pinnule.

The whole inner face of the axis and pinnules is ciliated (text-fig. 4), and the current produced by the cilia is the food-capturing mechanism. Each pinnule bears a band of short cilia, which is fringed with long laterals—hence a virtual groove results. This leads into the collecting axial groove, which has a zig-zag course down the filament. The four grooves of one side unite at their bases and lead directly into the sides of the proboscis likewise ciliated.

In the interior of these filaments is a tubular cavity in which a blood-vessel lies: these are described in the section dealing with "Internal Structure," but they can be seen in the living animal perfectly plainly.

When the animal is expanded the branchiæ are held in such a position that the two dorsalmost lie in the same straight line as the tube itself (text-fig. 3); hence the funnel is not arranged symmetrically round the tube-opening, but ventrally to it. The cilia produce a centripetal current, which is directed accurately into the mouth. It does not cause any water to enter the tube—in fact, there are tufts of cilia on the reflected face of the collar which specially guard against this.

The course of currents inside the tube is determined by the cilia on the body-wall and on the head. The tip of the head is ciliated dorsally, and there are two rows of long cilia at the back of the head (text-fig. 2), one being actually on the head (*cil.b.* 1) and one on the first thoracic segment between the insertion of the two angles of the collar (*cil.b.* 2). The current in the tube enters posteriorly, passes over the surface of the abdomen, then the ventral part turns dorsally round the hind edge of the membrane, and all passes out of the tube *via* the supra-thoracic canal. The course is demonstrated by taking a small piece of colony, or a few individuals in glass tubes, and adding finely-ground charcoal or stained starch-grains to the water (text-fig. 3).

Probably the thoracic membrane is of use in helping to direct this current, as it effectively confines the outgoing stream in the thoracic region to the supra-thoracic canal. In fact, any movement of water on the ventral side of the thorax is in a posterior direction, and is due to the suction action of the main current flowing round the hind edge of the membrane. The necessity for protecting this region from a strong outward flow is probably accounted for by the presence of a large mucous gland underneath the collar and first thoracic segments—the gland-shield (see p. 140), whose secretion would at once be washed away.

The tube-current will aid respiration, and also it disperses the anal excretion. The anus is terminal, but directed dorsally, hence the fæces are carried forwards to the opening of the tube. Here they are scattered, chiefly as a result of the beating of the head-cilia. In some cases the tube is notched dorsally, and when this is so the fæces are even more effectively removed. The spermatozoa on being discharged from the body are likewise carried out of the tube immediately by this current: the forward flow is seen when the ripe and discharging animals are watched, even after having been removed from their tubes.

Very similar in appearance to large stiff cilia are the palpicils. These are distributed singly over the dorsal edge of the collar and on the membrane and the tips of the branchial pinnules.

2. Phases of Life-history.

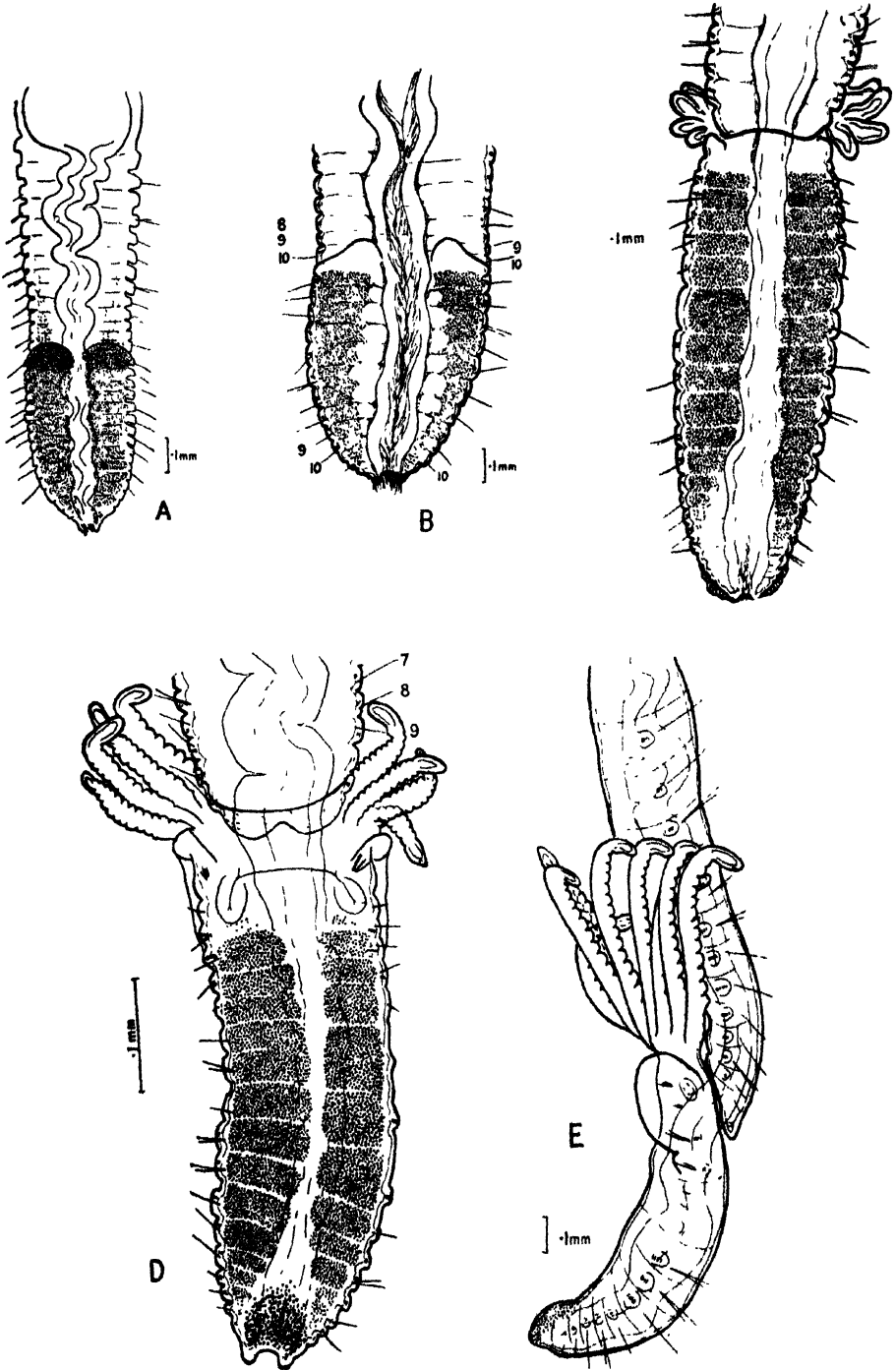
The description of external features must be supplemented by mention of those features which distinguish the various stages of the life-history. The

foregoing description may be taken to apply to a young individual, after the time when it first acquires the typical adult features and before it shows the first signs of reproduction. In addition to such individuals, some are found bearing a bud at their hind end, and others show signs of preparing to produce a bud or of recovering after having done so. The presence of sexual organs also modifies the appearance: they may be male only, or male and female both (in varying proportions)—this applies to the budding and non-budding worms equally. Also, eggs and embryos up to the age of settling are found in the tubes of the parent in great abundance during the summer. The statement of de St. Joseph (1894) that they are found inside the body of the parent—that it is, in fact, viviparous, seems to have no foundation. Hence every stage of the life-history is obtained by breaking up a small piece of the colony.

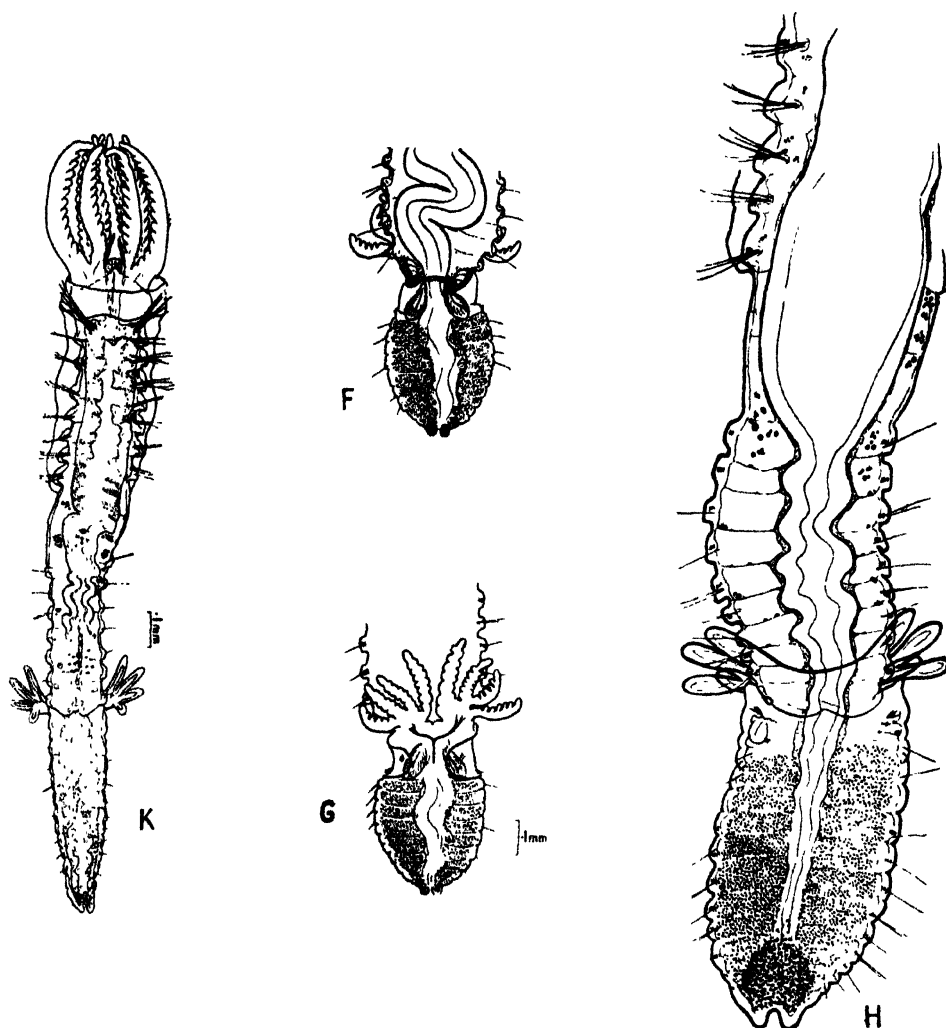
The relative proportions of these different forms depend somewhat on the time of year, the buds being more abundant during spring and early summer (February to July, at least) and sexual forms during summer and autumn. Budding can continue all the year, for even in mid-winter (December) a few isolated buds have been seen. During March, April, and May buds are extremely abundant. In the following three or four months buds are less abundant and the sexual forms mature. (At Naples, a sample taken on April 20, 1928, contained individuals with sexual organs practically mature.) After the sexual phase there follows a period of reduced activity during which buds are rare. In the summer, when budding and sexual reproduction are both possibilities, it is generally found that members of one colony tend to synchronise and pass through the same phase at the same time, though this is never strictly the case. A consideration of other Polychaetes suggested that the sexual organs might have a monthly rhythm coinciding with that of the moon, and, in order to test this, samples were collected regularly during a period of one month. The results obtained were negative, as the proportions of sexual and asexual individuals did not vary in any marked way.

The duration of the life of the stock and the number of asexual generations which may intervene between any two sexual cycles are two points which have not been determined, since observations are so difficult to make on tubicolous animals. Probably each individual has a sexual cycle at least once a year, but how many years an individual stock can last is unknown. There is evidence that an animal lasts into at least a second spring and begins budding again then (see p. 131). This arrangement, by which the sexual and asexual phases alternate, is different from the condition seen either in the Syllids, where the stock is asexual and the buds sexual, and doomed to perish, or from that seen in the Oligochaetes, where numerous successive generations of buds are produced and sexual phases are rare. To anticipate the description given later in the histological section, it may be mentioned here that when a bud is produced the tissues of the somites concerned are completely disintegrated and replaced by fresh ones. This process of histolysis, however, is not confined to the bud, but extends throughout the tissues of the stock (text-fig. 5K). Hence there seems to

TEXT-FIG. 5.



TEXT-FIG. 5 (cont.).



External features of the successive stages in the production of a bud. Figures drawn from life with the aid of a Leitz Zeichen-Okular.

- A. Dorsal view of hind end of a stock bearing a very young bud. B. Bud of same age as A as seen when focussed midway between the ventral and dorsal surfaces, to show coelomic cavities. C. Ventral view of slightly older bud, which possesses four pairs of simple branchial filaments. D. Slightly older bud with the branchiae pinnate and the anterior segments complete: both dorsal and ventral features are shown at region of junction of bud and stock. E. Lateral view of bud and hind end of stock; bud same age as in D. F. Ventral view of bud which has commenced to regenerate segments posteriorly, while the bud is still attached. G. Dorsal view of same individual. H. Dorsal view of stock bearing a bud of the same age as C, showing fat-globules in the coelom of stock. K. Stock with bud attached, showing an extreme case of degeneration of stock-tissues.

be a rejuvenation of tissues in the stock as well as in the bud at this time. In the Oligochaetes no comparable process has ever been described, but in view of the fact that they are capable of producing very large numbers of asexual generations in succession, without the interpolation of any sexual process, it would be of great interest to know whether any such mechanism for rejuvenation exists.

3. Configuration of Buds.

The buds produced by *Filograna* are terminal and single, and remain attached to the parent stock until all external developments and changes are complete and the bud has the appearance of a normal adult.

They are very variable in size when young, the number of initial segments varying between extremes of three segments and about twenty segments: when older there is much less variation, as proliferation of segments posteriorly compensates for any original lack. The position on the abdomen of the stock at which the bud is separated is equally inconstant. The various possibilities are discussed in the following section of the paper.

The processes involved in the formation of a bud have been partially described by Malaquin (1895 and 1905), and, as he states, they include both a transformation of old somites and a growth of new tissue. The head, branchiæ, collar, and next thoracic segment are all formed from new tissue proliferated anteriorly at the zone of separation of bud and stock. The following somites are formed by adaptation of the original terminal segments of the stock, while the most posterior segments are produced by the growing-point at the posterior end in the usual manner, after the commencement of the formation of bud. Hence there are two zones of active growth in a budding animal—one terminal and one at the level of origin of the bud-head. The latter not only produces the anterior part of the bud, but also a varying number of new somites anterior to itself: these will be the posterior segments of the stock after separation of the bud. The possibility of active growth taking place at a point removed from the hind end is a common feature in budding and regenerating Annelids. Strictly speaking, two separate processes of proliferation are in action at the plane of fission, as is shown below (page 183), one on the stock and one on the bud.

The first visible sign of the production of a bud (text-fig. 5) is the appearance of a pair of opaque pinkish masses lying at the sides of the gut, and extending throughout all the segments which will be concerned. These are formed by aggregations of both phagocytic and embryonic cells. Sometimes they extend even further forwards, gradually diminishing in size, into the somites which will remain in the stock. The transparency of the normal abdomen makes these conspicuous to the naked eye. Later a pair of prominences appear dorsally, the rudiments of the branchiæ, and the appearance of these determines the line of division between bud and stock. The lobes increase in size and each becomes bi-lobed; the right and left pairs then migrate laterally, remaining connected together by a transverse ridge of tissue—the rudiment of the new

prostomium. Still later a third lobe appears on each side, and these three filaments elongate considerably before the fourth, ventralmost, arises. At first the fourth is a rounded swelling at the base of the third, but later it becomes equal in size to the rest. From their first appearance these branchiæ are greenish, the colour being due to the presence in them of a broad blood-sinus.

Other less obvious, but equally important, changes take place in this region concerning the ventral and lateral portions of the new head. A circular constriction separates the bud from the stock, and, posterior to this, the new tissue laid down forms a complete ring, which, as it increases in size, separates further and further those two planes, now one on the stock and one on the bud, which at the beginning of the transformation were adjacent. The most anterior of this new tissue forms a ring projecting forwards and encircling the hind end of the stock dorsally and laterally, but remaining very small ventrally, where, as mentioned below, the anal papillæ of the stock develop, projecting backwards. Seen in lateral view (text-fig. 5 E) there is an overlap of the two individuals here, and a corresponding deep groove between them. This separation involves only the external tissues, as the gut and longitudinal muscles are continuous (though constricted) till the very end. The separation is increased by the growth of a certain amount of new tissue at the hind end of the stock, where a typical growing-point develops. The ventral and lateral portions of the rim of new tissue produce the proboscis (text-figs. 28 and 30), and, internally, the anterior parts of the blood and nervous systems. The proboscis thus encircles the old gut at the base of the angle which is formed as the separating constriction becomes deeper. The new tissue is laid down in such a way that from the first it has the form of a head and anterior region, and although this point has just been described as one of two growing-points which are active at the line of division, histologically speaking, it is not precisely similar to a terminal growing-point, but is rather of the nature of an active area. The actual amount of growth taking place here, as measured by cell-division, does not seem to be greater than at any other point on the bud, and the increase of tissue is rather the result of the accumulation of amœboid cells which wander into the head-lobes from the more posterior segments. (This is further described in the last section of the paper.) The difference is not very significant, and in any case it is difficult to imagine that atypical segments such as are present in the head-region could possibly be formed by the normal method of production of new segments. The differences in the two methods of proliferation are considered later from the point of view of "germ-layers."

Behind the branchiæ, in the enlarged base of the newly-formed tissue, the collar-chætæ appear, and at the same time, dorsally to them, a curved fold of the body-wall, which is the rudiment of the thoracic membrane. A second considerably smaller bunch of chætæ develops later on each side, and internally the coelomic cavities of the corresponding somites are outlined (text-fig. 5 H). Meanwhile, the parapodia of the most anterior of the old segments have been losing their chætæ and developing fresh ones. The most anterior of these

segments transformed belong to the abdomen while they are in the stock, but are thoracic when in the bud. Such a change entails a reversal in the position of the long chætæ and uncini. This interchange is beautifully illustrated in segments which happen to form the new chætæ before they lose the old ones, and so show the new long chætæ issuing from the same parapodial lobe that still bears some of the old uncini, or *vice versa*. Generally the old ones are completely lost first—in fact, there is often an achætous segment between the last new chætæ and the first old ones, representing the intermediate stage. The membrane is spreading posteriorly at about the same rate as the transformation of segments progresses. Apart from this change of place of the chætæ and the growth of the membrane, there is no other external change involved in the transformation of abdominal into thoracic segments. The external transformation proceeds more or less segment by segment from the anterior end in sequence, hence at any one time there is a gradation of stages along the animal.

A brief summary of the condition of a typical bud at a definite age, *e. g.*, one having its branchiæ in the form of four equal, elongated, but unbranched filaments (as in text-figs. 5 C and 5 H), will help to correlate the descriptions of the series of events happening in the various organs. The bud now is at the stage of having a newly-formed collar-segment and one post-collar segment: this is the newly-formed tissue, as contrasted with the transformed tissue, which comprises three or four segments bearing new small chætæ, also one or two achætous segments. Finally, there is the old unchanged posterior tip of the stock, together with any somites which may have been formed at the growing-point since the bud was defined. These, however, are not distinguishable with certainty.

In older buds, the changes already described are carried further. The branchiæ elongate and develop pinnules, and opercula also when these are present on the stock, so that, except for the fact that they do not bear cilia, they are precisely similar to those of the parent; the cilia do not develop until the bud is freed.

The transformation of abdominal into thoracic segments continues, probably, until the total number agrees with the number in the stock. As it is a practical impossibility to collect large numbers of buds at the moment of separation, it is uncertain how accurate is this correspondence. Counts made on old buds which are still attached have always (with one exception) shown the thorax of the bud to contain the same number, or fewer, segments than the thorax of the stock. Those with a smaller number are not significant, as they are probably still growing. The one exception showed a thorax in the stock of seven segments and in the bud of eight; hence it is apparent that the agreement is not absolutely precise.

Segments are constantly being produced at the growing-tip, so that the number of post-thoracic segments always remains somewhat greater than that of the thoracics. Finally, when the thorax is complete, the following two

segments lose their chætæ and remain achætous. Firstly, the long chætæ are lost, then the uncini, and, finally, the parapodial lobes. This process is not completed till after the bud is freed.

The next few somites sometimes lose their chætæ and develop new ones, but not always. This perhaps depends on the original size of the bud. If a bud begins, as it often does, with seven somites, these would all be taken over into the new thorax and transformed, but if it begins with fourteen somites, then the hind ones remain abdominal in the bud. It may be that these lose their chætæ and form new similar ones, in correspondence with the reorganisation of tissues taking place in these segments, while any segments formed after the commencement of budding form only the one permanent set.

The distinction between old and new tissue at the anterior end of the bud is marked by the presence or absence in the interior of the body-cavity of the mesodermal masses mentioned above. These appear as a double row of opaque blocks, and it is always easy to distinguish which segment bears the first of these: this is the first old somite. The most anterior block often diminishes in size, but it never disappears entirely (see text-fig. 5). Judging by histological evidence, this is due to the fact that its cells are passing forwards into the new tissue of the head. The comparative ages of the various somites is further indicated by the sizes of the chætæ. The first old transformed somite has the longest chætæ, and in the following somites the length gradually diminishes until the achætous condition is reached. Anterior to this, the collar-chætæ develop, but they remain much shorter than the anterior thoracic ones: the first post-collar somite develops its chætæ even later, hence they are always correspondingly smaller during growth-stages.

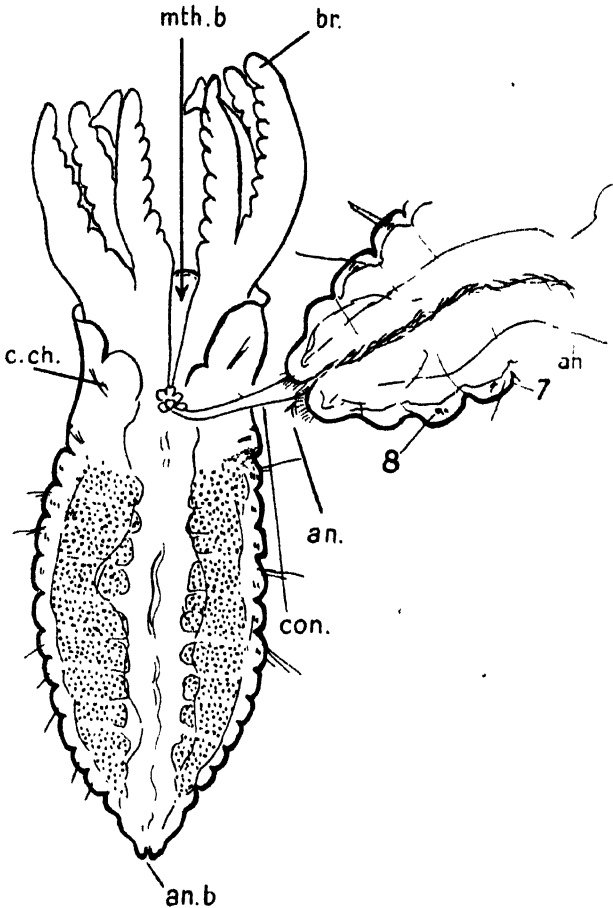
At the anterior end of the bud the collar has been growing laterally round the body, and the connection between bud and stock has become gradually narrower. Finally, only a slender connecting filament remains, and this is at last ruptured by muscular contractions of the two individuals. Text-fig. 6 was sketched from a bud which was watched while separation took place.

At the time of freeing the two halves of the collar are necessarily incomplete ventrally, but by the time that the last chætæ are lost from the achætous zone the collar is complete across the middle line.

The details of the changes which take place in order to permit the new mouth to function cannot be actually observed, but the general outline of events can be deduced from watching the living bud. The gut, so long as the bud is attached, is a continuous narrow tube. The new proboscis is laid down at the same time as the other head-structures, and hence is ready to function at the moment of freeing. The rudiment of the proboscis is the circular groove formed by the deep constriction separating bud and stock (text-figs. 5 F and 5 G). It has very thick walls, and they are so close together that a cavity is almost non-existent at this stage. When the bud is freed the internal edge of this groove joins with the old gut at the point of severance, and the whole now forms a continuous and functional structure; in text-fig. 6 this has already

happened. At the base of the new proboscis the old canal is replaced by new cells, and these are laid down in such a way that, when complete, a typical thoracic chamber results. The lumen enlarges at once to fill the body-cavity, and in the early stages this gives the gut a characteristic T-shape (text-fig. 7).

TEXT-FIG. 6.



TEXT-FIG. 7.

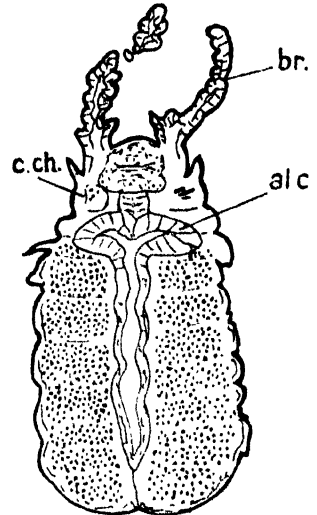


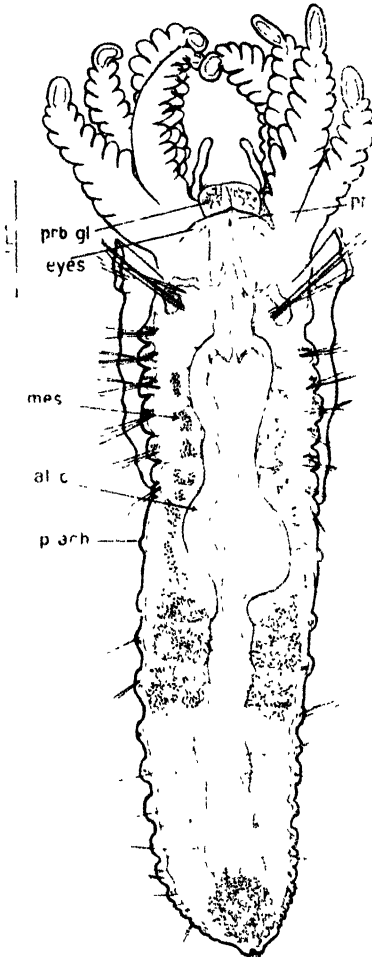
Fig. 6.—Bud and hind end of stock, at the time of separation of the bud (ventral view). *an.*, anus; *an.b.*, anus of bud; *br.*, branchiæ; *c.ch.*, collar-chætae; *con.*, connecting filament; *mth.b.*, mouth of bud.

Fig. 7.—Horizontal section through bud recently freed, showing the characteristic T-shaped gut. *br.*, branchial filament; *c.ch.*, collar-chætae; *al.c.*, alimentary canal, the broad anterior part being new regenerated tissue.

As the new wider canal is laid down it gradually encroaches on the old gut until the whole of the thoracic region has been replaced. By this time it has almost the normal appearance of a thoracic gut, though it is not yet pigmented, as it is in older individuals. The swollen region of the gut in the achæstous

zone is formed still later. It seems that the high columnar epithelium of the thorax is continued into this region, and afterwards, as the cavity becomes distended, assumes the cubical form.

TEXT-FIG. 8.



TEXT-FIG. 9.

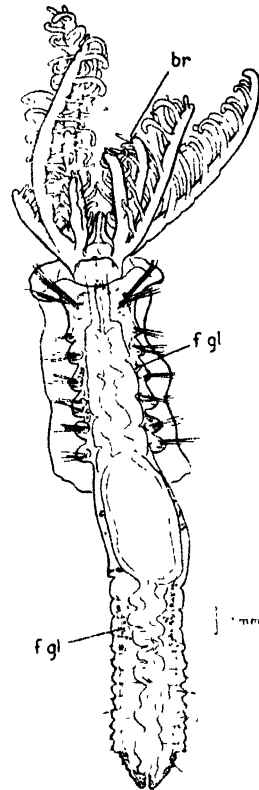


Fig. 8.—An individual which has recently been freed as a bud; drawn from living animal. *al.c.*, alimentary canal; *mes.*, internal mesodermal blocks; *p.ach.*, vestiges of parapodia on the achætosous zone; *pr.*, prostomium; *prb.gl.*, proboscis-gland.

Fig. 9.—A stock which has recently produced a bud and is now regenerating its hind end; dorsal view from a living animal. *br.*, branchial filaments, apparently regenerating after injury; *f.gl.*, fat-globules in cælom.

The mesoderm blocks are still conspicuous at the time of freeing, but gradually, as the wide thoracic gut is extending posteriorly, they diminish, and at last all trace of them is lost.

The characteristic appearance of the gut and the persistence of the mesodermal blocks indicate at a glance a recently freed bud (text-fig. 8). Another less conspicuous distinguishing feature is the fact that the glandular sacs (see p. 167) are at first not pigmented. The flame-like cilia, however, can be seen in action while the bud is still attached (text-fig. 5 H).

External changes in the stock are slight compared with those in the bud. The anal papillæ are formed, and sometimes, though not often, two or three segments are regenerated by this growing-point while the bud is still attached (text-fig. 5 F). When this is so there is a sudden transition between the old and the new tissue: the few recently added somites are smaller and narrower than the old ones, are more transparent, and have smaller chætæ (see Table I., col. i., last five individuals). After the separation of the bud this regeneration of the posterior end continues, and for some time the conspicuous difference between the old and the new somites persists (text-fig. 9). The absence of the anal glandular patch at this stage is mentioned below (p. 170).

The whole process of bud-formation takes place in a short time. On one occasion a few budding individuals were isolated in a finger-bowl. In twenty-four hours all the buds had separated, one, which was at the very earliest stages on the previous day, having been just recently freed.

4. *Grouping of Segments considered numerically.*

The facts which have been recorded on budding in Annelids show that in Polychætes the position on the stock at which a bud separates is usually a fixed point. Among the Syllids (Allen, 1921 and 1927, and Malaquin, 1893) there is a striking constancy in the position of the plane (or planes) at which fission occurs, "non seulement chez les différents individus d'une même espèce mais aussi chez les espèces différentes et même chez plusieurs genres" (Malaquin). In the case of the Oligochætes there is regularity of some definite kind often, but this does not necessarily mean constancy. There is even in the case of *Ctenodrilus* a plane of fission between each of the somites. In *Filograna* there is neither the constancy that is seen in the Syllids nor is there unlimited variation, but a more or less controlled condition intermediate between the two.

Before counting the somites it is obvious at a glance that there is much variation in the size of the buds: by counting accurately the somites in large numbers of budding stages a certain amount of order is found among them.

Now that the general evolution of the form of the bud has been described, the essential features (essential from the numerical point of view) of the origin of, and the series of changes in, a budding worm may be summarised and represented by a numerical formula. This permits tabulation of the results and so facilitates the comparison of large numbers of individuals.

The segments in the different regions of the body are counted from the anterior end, but in the majority of cases the two achæitous segments are omitted,

When this is so it is an indication that they are normal: if they happen to be abnormal, i. e., to bear parapodia or chætæ, they are inserted between brackets.

The zones are differentiated thus, *e. g.*,

collar 1. rest of thorax 7. abdomen 14.

In the case of a budding animal, the abdominal segments in front of the bud, and those included in the bud, are counted separately, the level of the head of the bud being indicated by an & sign: *e. g.*, 1 . 7, 8 & 8 (eight segments in the bud and eight in the abdomen of stock anterior to bud).

In cases in which the two sides do not correspond the $\frac{1}{2}$ sign is used, as, for example, a thorax with 7 parapodia on the right and 8 on the left, and a correlated inequality in the achætous zone (2 achætous segments on the right and 1 on the left) is formulated 1 . 7 $\frac{1}{2}$ (1 $\frac{1}{2}$), etc. Such a thorax is in process of extending itself posteriorly by means of a re-commencement of the process of transformation of somites, similar to that described above (see p. 124). When this happens, the first achætous segment develops chætæ, and to compensate for this the first abdominal segment becomes achætous. An animal which has recently added to its thorax in this manner (as indicated by the small size of the last thoracic chætæ) is formulated thus: 1 . 7 . 1, etc. Further, when the abdomen still has an obvious transition between the regenerating tip and the rest of the abdomen the numbers counted on the two regions are separated by a + sign.

The various kinds of individuals found represent the different stages of the life-history, and they can be arranged in the following classes:—

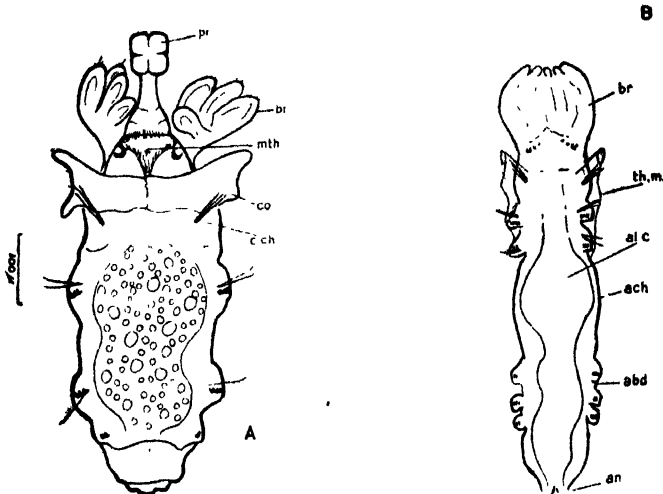
- A. Young individuals between the time of settling of the larva and the production of the first bud.
- B. Budding forms with no sexual organs present
 - (a) during the first budding season,
 - (b) during subsequent seasons.
- C. Stocks recovering after having produced a bud.
- D. Buds after freeing, still showing signs of their origin.
- E. Sexual forms.
- F. Budding forms with sexual organs in the stock.

CLASS A.

The young individuals settle when they possess the first three segments (as counted by chætæ) and build the tube (text-fig. 10). The next somites formed are at first abdominal, but the anterior ones become transformed into thoracic or achætous segments, in the same way that this happens in the bud. Segments continue to be formed posteriorly until the abdominal segments number approximately twice as many as the thoracics. When this stage is reached the posterior half of the abdomen may be separated as the first bud: however, embryos produced early in the summer may enter at once another sexual phase. Some larvæ which were kept in an aquarium during one winter reached this

stage in about six months : they settled and built their tubes in August, and in the following April all were producing buds. It is a peculiar fact that adults brought in from the sea and kept in an aquarium always come out of their tubes in a few days and lie on the floor of the tank ; but on two occasions when embryos were placed in finger-bowls they settled down, and not only built tubes, but stayed in them indefinitely. It was found by Orton (1914) that individuals only 4 weeks and 2 days old produced buds, and others at 11 weeks contained fully-developed eggs. Such young sexual individuals probably correspond to the small sexual animals mentioned above and to the last two formulated in Table IV., though the exact age of these is not known.

TEXT-FIG. 10.



A. Larva immediately after settling (length, 700 μ). B. Larva one month after settling.

abd., abdomen; *ach.*, achæteous zone; *al.c.*, alimentary canal; *an.*, anus; *br.*, branchiæ; *col.*, collar; *c.ch.*, collar-chætæ; *mth.*, mouth; *pr.*, prostomium; *th.m.*, thoracic membrane.

CLASS B (a). (Table I.)

The level at which the first bud appears is not constant, but there is a tendency for it to occur in such a position that the three regions (thorax, abdomen, and bud) contain all more or less the same number of segments. Such a case is expressed by the formula 1 . 7, 7 & 7, at its very earliest stage, before there is any activity at the growing-point.

CLASS C. (Table II.)

In the case of animals budding in the first season recovery of segments takes place as described above.

CLASS D.

The general appearance of the buds after freeing has been described also (p. 128): for purposes of this section of the paper, they are identical in their behaviour with sexually produced forms of the same size (Class A), and require no special mention.

CLASS E. (Table IV.)

The characteristic feature of this stage of the life-history is the great length of the abdomen. There are commonly about forty somites, of which the anterior are swollen and tense with a mass of genital cells, and the posterior are clear and flexible. During autumn young individuals are found containing sexual organs: these are presumably sexually-produced individuals which at once enter another sexual phase, without passing through an intervening asexual phase. In the late autumn, when the sexual season ends, there is a period of inaction until the following spring, when budding begins again.

CLASS B (b).

Just as in the buds of Class (a), there is here, again, a tendency for the plane of fission to be so situated that the number of abdominal segments before it and behind it are more or less equal to each other (though not to the number in the thorax in this case). Hence, as the abdomen in these individuals which have passed through a sexual phase is very long, it follows that the buds of this class are also abnormally long: frequently they possess twenty initial segments. In other respects they resemble those of class B (a). (Individuals of this type occur only in spring; they are included in Table I., column iii.)

CLASS C. (Continued from above.)

As regards the stock of these second-season buds, it appears that there is not necessarily an immediate regeneration of posterior segments. These stocks commonly possess about twenty abdominal segments, and abdomens of this length are not seen with regenerating posterior ends. On the other hand, it is very common to find them budding, dividing more or less accurately in half, and thus producing an animal of such a type as 1 . 7, 10 & 10. Individuals of this type, (included, with others, in Table I., column ii.), occur in spring.

CLASS F. (Table III.)

Buds arising on abdomens which contain sexual organs are similar in their origin and development to those of class B: the sexual cells may occur in any or all the segments of the abdomen of the stock. They are never abundant, and, in the case of the ova at least, always remain small and immature; the sperms appear to be mature, however.

The preceding facts have been summarised from tables of figures (Tables I.-IV.) derived from samples of colonies taken at random from all possible collecting-grounds at all seasons of the year.

The counts of buds refer to the very young stages, unless otherwise stated, before there has been any proliferation of segments posteriorly at the growing-point. In the exceptional cases for which older buds have been used, the age is given in terms of the branchiæ on the bud-head. The number of branchial lobes is given (in pairs), and if the bud is sufficiently old to have the filaments pinnate, this is mentioned.

In the earliest stages of budding it is sometimes very difficult to decide precisely where is the dividing-line. In many cases there is no doubt, as the mesodermic blocks are accurately confined to the bud-segments and are definitely either present or absent; in other cases they diminish gradually, and this may introduce an error of ± 1 or even 2 segments.

A large number of buds conform more or less accurately to the type of formula mentioned above, viz., 1.7, 7 & 7, but others tend to group themselves in the manner described as applying particularly to the buds of class B (*b*). Formulæ of the former type have been collected into Table I., Column i., and those of the latter into Table I., Column ii. A third possibility is that the numbers of segments in the different zones may be multiples of, instead of equal to, each other, *e. g.*, 1.7, 14 & 7: such formulæ are grouped into Table I., Column iii. There are still other combinations of numbers which do not seem to fall in with any devisable scheme. This is not surprising, considering that there is so much variability in the behaviour of these animals, and that even in the "typical" cases there is often not absolute accuracy in the numerical relationships, but possibly a divergence of ± 1 or 2 segments from the theoretically calculated number. [The possible error in making the counts must also be considered.] These aberrant cases are placed in Table I., Column iv.

Table I.—INDIVIDUALS OF CLASS B.

Buds (of 1st and subsequent seasons) arising on asexual Stocks

Column i.

1.5	5 & 4	1.6	8 & 8
1.5	7 & 6	1.6	4 & 6
1.6	6 & 6	1.6	7 & 7
1.6	5 & 6	1.6	6 & 8
1.6	5 & 4	1.6	7 & 7
1.6	7 & 6	1.6½ (1½)	8 & 8
1.6	8 & 5	1.6½	6½ & 8
1.6	8 & 7	1.7	7 & 7
1.6	8 & 7	1.7	7 & 7
1.6	8 & 7	1.7	7 & 7

Table I. (*continued*).Column i. (*continued*).

1.7	7 & 7	1. 7½ (1½)	8 & 8	
1.7	7 & 7	1. 7½	7½ & 9	
1.7	7 & 7	1. 7. 1	8 & 10	
1.7	7 & 7	1. 8	8 & 6	
1.7	7 & 7	1. 8	8 & 8	
1.7	7 & 7	1. 8	8 & 9	
1.7	7 & 6	1. 8	9 & 8	
1.7	7 & 6	1. 8	8 & 9	
1.7	7 & 8	1. 7. 1	6 & 10	} 4 branchial lobes.
1.7	5 & 7	1. 8½	9 & 11	
1.7	6 & 8	1. 9 (1)	8 & 9	
1.7	8 & 7			
1.7	7 & 5	1. 7	6+2 & 15	} branchiæ pinnate.
1.7	8 & 9	1. 7	7+1 & 15	
1.7	8 & 8	1. 7	7+3 & 14	
1.7	7 & 8	1. 7	6+3 & 11	
1. 6. 1 (1)	6 & 6	1. 7	7+1 & 15	

Column ii.

1. 6	10 & 11	1. 7	10 & 11
1. 6	10 & 11	1. 7	4 & 4
1. 6	12 & 11	1. 7	9 & 10
1. 6	11 & 9	1. 7	19 & 18
1. 6	3 & 3	1. 7½	12 & 11
1. 6	10 & 10	1. 7	10 & 12
1. 6. 1	9 & 9	1. 8	10 & 10
1. 6. 1	9 & 9	1. 8	11 & 10
1. 6. 1	10 & 10		
1. 7	10 & 10	1. 6½	10 & 8
1. 7	10 & 10	1. 7	8 & 10
1. 7	10 & 10	1. 7	8 & 10
1. 7	10 & 10	1. 7	12 & 10
1. 7	11 & 11	1. 8	12 & 9
1. 7	11 & 10	1. 8	12 & 9
1. 7	10 & 11	1. 8	10 & 8

Column iii.

1. 5	10 & 12	1. 6	12 & 17
1. 5. 1	10 & 6	1. 6	12 & 14
1. 6	12 & 3	1. 6	12 & 14
1. 6	17 & 13	1. 6	12 & 14

Table I. (*continued*).Column iii. (*continued*).

1.6	12 & 10	1.7	14 & 14
1.6	6.6 & 13	1.7	15 & 7
1.6	13 & 9	1.7	13 & 14
1.6	11 & 9	1.7	20 & 18
1.6	13 & 11	1.7	14 & 15
1.6	18 & 9	1.7	16 & 19
1.6	18 & 14	1.7	15 & 12
1.6 $\frac{1}{2}$	11 & 6	1.7.1	17 & 8
1.6.1	15 & 16	1.7.1	13 & 13
1.6.1 (1)	7 & 11	1.7 $\frac{1}{2}$	19 & 11
1.6.1 (0)	19 & 6	1.7.1	13 & 18
1.7	15 & 8	1.7	14 & 17
1.7	14 & 6	1.8	26 & 7
1.7	16 & 8	1.8	15 & 9
1.7	15 & 3	1.8	16 & 8
1.7	14 & 9	1.8	16 & 6
1.7	14 & 15	1.8	14 & 21
1.7	14 & 6	1.8	12 & 6
1.7	14 & 17		

Column iv.

1.6	8 & 4	1.8	7 & 5
1.6	15 & 4	1.8	9 & 5
1.5	8 & 5	1.7 $\frac{1}{2}$	12 & 9
1.7	11 & 4	1.8	13 & 10
1.7	6 & 4	1.8	13 & 9
1.7	17 & 9	1.8	10 & 4
1.7	13 & 9	1.8	18 & 23
1.7	18 & 10	1.9	13 & 6
1.7	16 & 3	1.9	11 & 4
1.7	7 & 2	1.9	7 & 4
1.7.1	11 & 8	1.9	11 $\frac{1}{2}$ & 6

Table II.—INDIVIDUALS OF CLASS C.

Regenerating Stocks.

1.5	19	1.5.1	22
1.6	11	1.6.1	17
1.6	10	1.6.1	20
1.6	21	1.6.1	13
1.6	12+4	1.6.1	20

Table II. (*continued*).*Regenerating Stocks (continued).*

1.7	14+5	1.7	10
1.7	15+2	1.7 (0)	10
1.7	15+2	1.7	7+4
1.7	14	1.7	6+4
1.7	28	1.7.1 (1)	6+3
1.7	27	1.7	20
1.7	21+2	1.7.1	14+2
1.7	7	1.7½	15
1.7	7+10	1.7.1 (1)	16
1.7	7+2	1.8	8+2
1.7	11+3	1.8	10
1.7	12+3	1.9	13
1.7	12+1	1.8.1 (1)	6+3 (with young ova).

Table III.—INDIVIDUALS OF CLASS F.

Buds arising on Sexual Stocks.

1.8	17 ♂	& 13 (4 branchial lobes in bud).
1.7	8 ♀	& 17 (branchiae pinnate).
1.8	13 ♂	& 5 (very young bud).
1.7	8 ♂	& 12 (4 branchial lobes).
1.6½	6½ ♂ & ♀	& 14 (4 branchial lobes).
1.6½	12½ ♀	& 12 (very young bud).
1.7	6 ♀	& 8 (very young bud).
1.7	7 ♀	1 asexual & 10 (4 branchial lobes).

Table IV.—INDIVIDUALS OF CLASS E.

Sexual Forms.

	♂.	♀.	Asexual.
1.7	8	0	10
1.7	2	3	10
1.7	2	8	16
1.7	2	12	24
1.7	2	15	25
1.7	2	11	?
1.7	2	12	25
1.7.1	2	6	10
1.6	2	12	20
1.6	1	10½	25
1.5	2	10	21

Table IV. (*continued*).*Sexual Forms (continued).*

1.8	1 ♂	1 ♀	6 ♀	5 asexual.
1.7 1 ♂	$\frac{1}{2}$ ♀	$5\frac{1}{2}$ ♀	9	"
1.7	$8\frac{1}{2}$ ♀		$11\frac{1}{2}$	"
1.7.1	(1)	10 ♀	10	"
1.6.1	(1)	7 ♀	9	"
1.7	4 ♀		13	"
1.7.1	(1)	18		sexual, young.
1.6.1	(1)	14		" "

From these results certain conclusions may be drawn concerning the nature of the factors which determine the initiation of bud-formation. In cases such as the Syllids, in which there is absolute constancy in the position on the stock at which a bud originates, no suggestion as to the reason of this can be given, whereas a variable type such as *Filograna* offers data from which certain facts may be deduced.

Apparently the somites are all equivalent as regards potentiality to produce the bud-head and plane of fission. Determination of the position of this depends upon the parent individual considered as a whole, from the point of view of size, size of the thorax, age, and phase of the life-history. Hence it follows that in any individual there are certain probable potential planes of fission, and, as an individual changes its size as a result of increase by growth, or decrease by budding, so the positions of these planes move, and the buds produced successively by a given stock may originate from different levels along the abdomen of that stock.

There is a more or less vague anterior limit before which a bud never arises. It is rare to find a budding individual in which the abdominal segments anterior to the bud-head are fewer in number than those in the thorax, and in no case has a bud been found anterior to the fourth abdominal segment of the stock.

In spite of the repeatedly mentioned contrasts between *Filograna* and the Syllids, this general conclusion is in harmony with the observations derived from the Syllids—and further, with results obtained from regeneration experiments on other Polychætes. For instance, the behaviour of Syllids in regeneration, as described by Allen, illustrates the fact that every somite has a certain individuality dependent on its numerical position in the metameric series of the whole animal—in fact, this character is developed to an extreme, and the numerical phenomena are accurately precise. The results of Berrill (1928) on regenerating *Chaetopterus* show similarly that each segment regenerates according to its position on the stock.

The fact that potential planes of fission occur along the abdomen separated from each other by equal (or rhythmical) intervals is a peculiarity of *Filograna*. A parallel case of this phenomenon is given by Potts (1913) in a description of

a *Trypanosyllis*: the individual in question possessed scars marking the position of successive planes of formation of buds in three places, these being separated by equal intervals along the abdomen of the stock.

The most outstanding impression that remains after reviewing the various kinds of ways in which buds are formed in Annelids is that the case of *Filograna* is probably one of the most highly evolved and complex of them all. Johnson (1902) states that the collateral type of budding as seen in *Trypanosyllis* is "unquestionably the most specialised mode of asexual reproduction, not only among the Syllidæ, but among all known Annelids," and it is probably equally true that *Filograna* is the most specialised of those which produce linear buds. This conclusion is indicated by two points: firstly, by the great amount of regeneration that the tissues undergo at the time of budding, and the precocious commencement of this process: and, secondly, by the fact that the head is the first portion of the bud to be differentiated. In the simpler fission-type of budding this is not so, as, for example, in *Æolosoma* (Hämmerling, 1924, 1) and some of the Syllids, and in *Filograna* it is probably a secondarily acquired character, evolved in order to allow the more complex structures to be completed at the same time as the less complex, and paralleled in many embryological developments.

In *Oligochætes* there is at least one genus (*Lumbriculus*), which on stimulation separates its posterior end autotomously. The budding in other *Oligochætes* may reasonably be regarded as a phenomenon of this nature, more or less specialised in so far as the head is formed at the zone of fission at some time before rupture takes place.

Description of Two Abnormal Buds. (Text-fig. 11.)

Two abnormal cases of bud-formation have appeared during the course of this work. The abnormality in both these is precisely the same, and the two are of the same age: hence they are almost identical. They occurred at different times (several years apart, in fact) and were both found among material freshly brought in from the sea (*i. e.*, not more than two days in the tanks). Both were fixed in Bouin's fluid and sectioned in a horizontal plane.

The peculiarity of these two lay in the fact that a bud-head was being produced terminally at the posterior tip of the stock. Four pairs of branchiæ and a head-lobe were present in each, hence the age corresponds to that of the normal individual figured in text-fig. 5 C. In case 1 there were 11 somites in the abdomen of the stock, and in case 2 there were 5, all containing young oocytes.

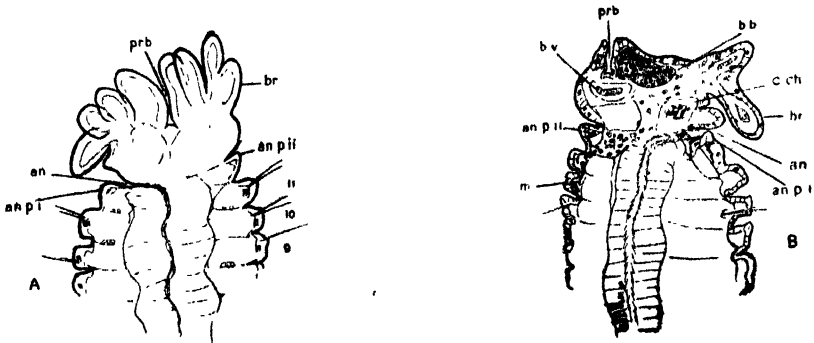
The rest of the description may be taken to apply to either individual equally.

The sections confirmed a fact that was suggested by the living animal, namely, that the complete bud was being produced on one half only of the stock. On one side of the animal was a normal anal papilla: on the other side was also an anal papilla, but on its mesial (or anal) face was a large outgrowth of new tissue, bearing the growing branchial filaments and containing a mass of tissue

attempting to form a new head. The interior of this mass contained a brain, blood-spaces, a proboscis-tube, and the first pair of chætal sacs. The anus is displaced from its median position by this new lobe and opens laterally.

The two peculiarities of this bud—namely, the terminal and the unilateral origin of the bud-head—are both features very rare in Annelids. No reference to naturally occurring terminal buds can be found; but comparable biaxial heads are mentioned by Hyman (1916) as arising among Oligochaetes in experiments on regeneration. As regards the unilateral position of the bud—though this is rare as an abnormality, yet, on the other hand, it is the rule in the species *Syllis ramosa*, and there is a comparable condition described as collateral budding in *Trypanosyllis* (Johnson, 1902). There is, further, a record of the production of a double head (which is probably comparable) in *Typo-syllis* (Langerhans, 1881), and similar double heads are described also in Oligochaetes under experimental conditions by Hyman (*ibid.*).

TEXT-FIG. 11.



Abnormal terminal bud. A. Sketch of external appearance of bud-head.

B. Horizontal section through same region.

an., anus; *an.p.i.* & *an.p.ii.*, anal papillæ of stock; *b.b.*, brain of bud; *br.*, branchiæ of bud; *c.ch.*, collar-chæta; *m.*, muscles of stock; *prb.*, proboscis of bud; *b.v.*, blood-vessel; figures indicate segments counted from anterior end of abdomen of stock.

ALIMENTARY CANAL.

The alimentary tract is a simple tubular canal, whose walls are formed by a single layer of epithelial cells: external to these cells is the peritoneum—the interval between the two being filled with blood. Further, in the anterior half, between the mouth and the hind end of the achætatus zone, the walls are invested with a sheath of circular muscle-fibres lying outside the blood-sinus. The cells forming the wall of the canal are all ciliated, but, by reason of certain histological changes in the character of the cells and of changes in the size of the lumen, four anatomical regions are distinguishable.

The funnel-like mouth leads into the tubular proboscis, which extends as far

back as the middle of the collar-somite. Here it forms a bulbous swelling and opens into the much wider thoracic chamber, which almost fills the body-cavity. The lumen enlarges even more in the achæitous zone to form the very capacious third chamber whose walls lie close against the body-wall and may even distend this. On entering the abdomen, the canal narrows again suddenly to a comparatively slender tube, the intestine, which passes in a sinuous course to the anus.

The canal in the thoracic and achæitous zone is darkly pigmented, but in the abdomen is almost colourless. Very frequently the canal is empty, but at other times the large anterior chambers contain masses of structureless debris, which is kept constantly in rotation as a result of the action of the cilia.

Mitotic divisions of the ciliated cells are often seen at the anterior end of the thorax, in the neighbourhood of the lateral angles of the chamber. Between the most posterior cell of the gut and the adjacent epidermal cell (the junction being marked by the termination of the cilia) is a pair of large vesicular pear-shaped cells.

BODY-WALL.

The body-wall is composed of :—

1. Epithelial cells in a single layer, with the cuticle secreted by them externally and their basement-membrane internally.
2. The muscular layer—longitudinal only in some places and longitudinal and circular in others.
3. The central nervous system, since this is in close connection with the epidermis throughout.
4. The somatic peritoneum.

1. *Epithelium.*

The epithelial cells vary greatly in form and size in different parts of the body, and cells of special function (*e. g.*, glandular etc.) occur in places; the several varieties of these cells will be considered in order. Some of these observations have been made on living animals, aided at times by the use of intravital stains, others are based on sectioned material.

Ciliated Cells.—The ciliated areas of the body-wall are in only a few cases of the nature of a true ciliated epithelium; for the most part they are merely typical cubical or columnar epithelia, in which isolated ciliated cells are scattered. The actual ciliated tracts are restricted to the branchial grooves, the dorsal surface of the tip of the head, and two transverse bands at the back of the head (text-fig. 2, *cil.b.* 1, and *cil.b.* 2). These cells on the head are the largest of all the ciliated cells, being tall and slender. Their bases are branched (text-fig. 20), and they stain very darkly with Heidenhain's iron hæmatoxylin. On the thorax and abdomen the ciliated cells are similar in size and appearance to the other cells of the epithelia in which they are situated: hence they are much smaller on the abdomen than on the thorax.

Notochordal Cells.—The branchial axis is formed by clear colourless cells : these are rectangular in shape, and arranged in perfectly regular rows along the external face of the axis. At the base of the branchiæ they become more polygonal, and, finally, after the union of the four filaments, are shaped like scallop-shells. In surface-view the cells on the axis have a diameter of $50\ \mu$, but the larger ones at the base may reach $100\ \mu$. These cells are very similar to those described by Giroud and Gleize Rambal (1925) in other Serpulids. They are almost transparent both in living and in fixed material, but show a delicate honeycomb in their interior. In life this is greenish ; in sections it is seen to be formed by lamellæ crossing the cavity, mostly parallel to the long axis of the cell. The protoplasm is small in amount and forms a border to the cell on its outer face : in this the nucleus is situated (text-fig. 4 A). The rest of the cell is filled with large clear vacuoles, and no doubt the fluidity and turgidity of these cells give them value as a flexible skeletal support to the axis, somewhat of the nature of a notochordal rod. These cells are referred to by de St. Joseph as mucous cells, but they do not give the reactions of mucous cells.

Other cells, similar to but not identical with these, occur in other parts of the body, particularly in those parts of the body-wall where movements of flexion take place. There is a broad band of these cells along each side of the thorax, in the region of attachment of the thoracic membrane. This provides a firm basis for the attachment of the membrane, and probably serves as a kind of hinge-joint at its base. Then, also, similar cells compose the anterior wall of the uncinal lobe of the parapodia. The suggestion that these have a comparable significance is discussed on page 150.

There are two other patches of absolutely clear vacuolated cells. These form a pair of club-shaped areas at the junction of the lateral part of the collar with the gland-shield area of the body-wall. They slope obliquely ventrally and laterally, and reach the external surface both laterally at the front of the gland-shield and mesially at the base of the V-shaped angle between the collar and the proboscis-wall (text-fig. 19). The actual use of these patches is not obvious, but, as in the other cases mentioned above, their position marks a joint—in this case it is the line of union between collar and body, just where a hinge-like movement will occur when the collar-muscles are in action. Perhaps the vacuoles act as a cushion to absorb the compression-strain which would otherwise be exerted on the surrounding cells. The particular cells which would be subject to the strain would be the goblets of the gland-shield, and this vacuolated patch may be a device to protect these.

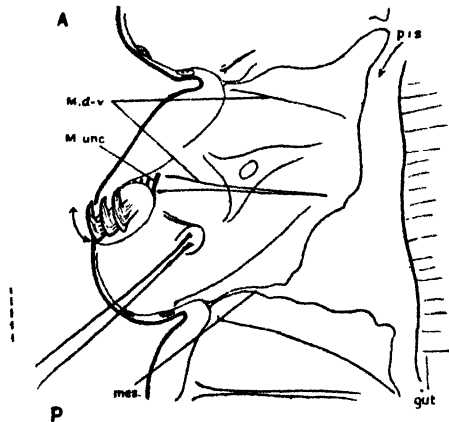
Glandular Cells.—These occur in several areas, viz., a gland-shield ventrally on the collar and succeeding somite, patches on the branchiæ, a patch in front of, and dorsal to, the anus, and two pairs of glandular areas of the proboscis—in addition there are in places isolated mucous cells.

The gland-shields are swollen areas forming the ventro-lateral body-wall from the level of the insertion of the collar (even extending on to the collar) to the hind end of the sub-œsophageal ganglion—or slightly behind this (text-

figs. 14 and 20). The area extends mesially as far as the mesial edge of the ganglion, and laterally as far as the base of the collar-notopodium. It is subdivided on each side into four quadrants, as the result of the passage through it of the muscle *M.e.c.* 2 longitudinally and the posterior nerve and the blood-vessel of the collar transversely. All these structures lie superficially, immediately beneath the cuticle, and hence among the glandular cells. The gland-shields are composed of goblet-cells, which have long stalk-like bases staining an intense blue with iron hæmatoxylin. The contents of the goblets stain bright red with Mayer's mucicarmine, and yellowish with iron hæmatoxylin. Hence it is concluded that this is a mucous gland.

Isolated mucous cells are found in those regions of the epidermis which are provided with cilia. There are two lateral rows in the abdomen beneath the

TEXT FIG. 12.



Horizontal view of abdominal parapodium, seen in the living animal.

M.d.v., dorso-ventral muscles; *M.unc.*, uncinal muscles; *mes.*, mesentery; *p.i.s.*, peri-intestinal sinus; A. & P. indicate anterior and posterior

nerve-cords, and a few laterally in the achætoous zone. The only other cells which are affected by mucicarmine are the glandular patches on the branchiæ at the bases of the pinnules (see text-fig. 1). These take on a pinkish tinge much paler than that of the goblet-cells; however, on the pinnules themselves are a few isolated cells staining a dark dull red (also among the cilia). The behaviour of food-particles when being captured by the branchiæ suggests that they are being captured by some sort of viscous solution; hence it is probable that these are the cells responsible for producing it.

Four patches of glandular cells, two dorsal and two ventral, occur on the proboscis (text-figs. 8 and 26). They are composed of tall granular cells, but at present no special function has been ascertained for them.

The anal glandular patch is a rather loosely defined aggregate of cells situated

in the dorsal body-wall just anterior to the anus. It is broadest posteriorly (text-figs. 5 and 8); anteriorly it tapers and becomes diffuse, gradually merging with the other epithelial cells. Single lobate cells similar in appearance to these composing the gland occur all along the ventral surface of the abdomen. When stained intra-vitam with methylene-blue the nuclei of these cells under some conditions show a deep red colour. This gland is further described in the section on "Excretion," as it appears to function as an excretory organ.

Pigment.—The pigmented portion of the epidermis is restricted to the head and anterior segments of the thorax. The pigment is distributed in the form of small orange-red granules round the margin of the epithelium-cells on the intercellular boundaries, immediately underneath the cuticle.

The chaetal sacs are of two kinds (text-figs. 12, 16, and 17), one bearing long chaetae and the other uncini. The former is a deep finger-shaped sac with a bifid base, from each branch of which a bundle of bristles arises—the simple-shaped chaetae in one and the complex in the other; at the bases of the sacs are the setigerous cells. The base of the chaeta is closely invested by the cells of the sac, but the more distal part lies freely and projects through the mouth of the sac. In the case of the uncinal lobe the sac has lost its cavity and is reduced to a thickened ridge of tissue. In this the nuclei are embedded along the internal margin, one corresponding to each hook, but cell-outlines cannot be seen with certainty. In this ridge the uncini are deeply embedded, having only their distal hooks projecting beyond the surface.

2. *Musculature.* (See text-figs. 13–18, 20, 22.)

The musculature can be observed to some extent in living animals, both by examining the movements and by tracing the course of the fibres when a favourable individual is found. But the greater part of this subject has been worked out on serial sections.

The muscles can conveniently be grouped for purposes of description into six divisions, but these are purely arbitrary and have no functional significance:—

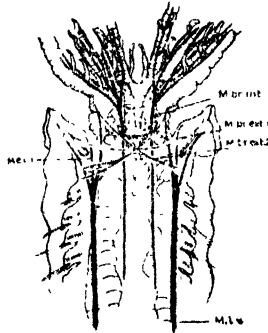
1. Musculature of the body-wall.
2. Branchial musculature.
3. Muscles of the thorax, collar, and thoracic membrane.
4. Septal and trans-cœlomic fibres.
5. Chaetal muscles.
6. Gut-muscles.

1. In the body-wall are longitudinal fibres grouped more or less into four zones or bundles: the concentration into distinct bundles is more pronounced in the thorax than in the abdomen. In addition to these four strands there is another pair of fibres, much smaller and inconspicuous. All the fibres extend from end to end of the animal and lie almost entirely against the basement-membrane of the epidermis. The four main bundles are separated from each

other by the parapodia laterally, the mesentery dorsally, and ventrally by the two nerve-cords and all that lies between them : alternatively, the facts could be described by saying that the continuous layer of muscles is interrupted by these structures. One pair of bundles, therefore, is dorsal (*M.l.d.*) and one ventral (*M.l.v.*) ; the small pair is also ventral (*M.l.m.* posteriorly and *M.pr.* anteriorly, as it extends into, and along, the proboscis). The individual fibres are parallel and ribbon-like, and no structure can be observed in them.

The only place where circular fibres can be found is in the achætatus zone : here isolated fibres are seen (*M.c.*) lying against the epidermis, and hence external to the longitudinal muscles and to the nerve-cords. The significance of the restriction of the circular fibres to this one zone is not obvious. As mentioned above, this region of the body generally appears more or less distended owing to the enlargement of the gut-cavity within it : immediately behind it there is

TEXT-FIG. 13.



Diagrammatic dorsal view of anterior end, to show musculature of head and branchiæ.

M.br.int., internal branchial muscle ; *M.br.ext. 1* & *2*, external branchial muscle ; *M.e.c. 1*, erector muscle of collar ; *M.e.ch.p.*, posterior erector of collar-chæte ; *M.l.v.*, ventral longitudinal muscle.

a sudden narrowing of the lumen, and this arrangement may cause perhaps a high pressure in the chamber anterior to it. As a result of the distension of the gut, its wall lies close against the body-wall, hence contraction of these circular fibres compresses not only the gut-cavity, but also the coelomic space surrounding it. It is possible that these circular muscles form a pumping mechanism to drive the blood contained in the peri-enteric sinus forwards into the branchiæ to expand them, or even that after the blood is driven forwards by the anti-peristaltic contractions of the gut-muscles, these body-muscles maintain a constant pressure to retain it there. Further, if, as was suggested, there is a high pressure of liquid in the gut, the increased resistance offered by the gut-contents to compression by the circular fibres would increase proportionately the effectiveness of the contraction in compressing the intervening blood-sinus.

External to the longitudinal muscles are a few transverse (*i. e.*, incomplete

circular) fibres, likewise situated externally to the longitudinal fibres. Some of these will be mentioned again in connection with the collar and chætal muscles. A few fine strands are found also in the ventral body-wall, lying close to, and external to, the nerve-commissures.

There is further one special anterior transverse fibre, which differs from those previously mentioned in that it lies internal to the longitudinal muscles. This lies posterior to the brain and anterior to the posterior ganglion of the brain (see text-figs. 20 and 22) and to the transverse bar of the blood-ring (*M.tr.a.*). Its lateral insertions are rather vague, but it turns forwards round the sides of the brain, and is gradually lost against the external sheath of the brain near to the fibres of the internal branchial muscle. This fibre may be concerned with effecting a contraction of this section of the blood-ring. As mentioned elsewhere, there are no muscles in the walls of the blood-sinuses, but these particular transverse fibres are in such close contact with the blood-vessel that this explanation seems possible. Further, this transverse part of the blood-system is almost always empty and collapsed in fixed animals, so much so that it is very difficult to trace often, while the lateral parts of the ring are swollen and obvious. If this explanation is correct, it is probable that the contraction of the blood-ring as effected by it serves to drive the blood round from the dorsal to the ventral vessel, rather than into the branchiæ.

The one position where the muscles are not in actual contact with the body-wall is in the collar-somite. Here the epidermis is raised into a ridge, and the muscles continue their straight course across the base of this. The space remaining in the ridge, external to the muscles, lodges the transverse duct of the glandular sac and the muscle-fibres *M.ch.tr.* and *M.br.ext.* 2.

Anteriorly the ventral strand subdivides into sections, and these are inserted into the branchiæ, the collar, and the anterior chætae.

2. The branchial muscles are the anterior terminations of the main longitudinal strands (with one small addition), and they include two distinct series.

Firstly, the dorsal muscles of the body-wall on each side pass over the brain to the antero-lateral angles of the head, and then continue into the base of the branchiæ, after which they are referred to as the internal branchial muscles (*M.br.int.*). Here each subdivides into four, one strand supplying each axis. In the axis it lies against the epithelium of the mesial face and sends a branch into each pinnule: in the case of operculate filaments it spreads out and forms a lining to the cavity of the cup.

The second, external, series of fibres is derived mainly from one of the anterior subdivisions of the ventral strand. The division occurs at the hind end of the suboesophageal ganglion, and the branchial section (*M.br.ext.* 1) passes obliquely dorsally, between the glandular sac and the epidermis, till it reaches the common base of the branchiæ. Here it is joined by a bundle of fibres which has arisen on the opposite side of the animal (*M.br.ext.* 2). These fibres arise against the basement-membrane of the dorsal epidermis at the back of the collar-somite (text-figs. 13 & 15): the fibres from the two sides cross one

another beneath the second transverse ciliated band, and then spread out broadly. Of the fibres thus separated some join the main branchial strand, while others pass almost directly forwards underneath the brain to the tip of the head, and a very few, running close to these, continue past the tip into the proboscis. The whole mixed branchial bundle thus formed lies at first against the basement-membrane of the clear axis-cells which form the external wall of the filaments. Almost immediately it inserts itself between these cells and comes to lie against the cuticle adjacent to the external nerve, *N.br.ext.* The

TEXT-FIG. 15.



Drawing of the anterior end obtained by superimposing consecutive horizontal serial sections, to show musculature, excretory organ, etc.; the right half is more dorsal (*i.e.*, superficial) than the left.

Lettering as in text-fig. 14. In addition:—*pr.* prostomium; *p.s.*, peri-enteric sinus; *cil.d.*, ciliated duct of excretory organ.

muscle almost at once becomes extremely small and is soon lost altogether. As mentioned above, the mechanism which effects the straightening, or extension, of the filaments is probably a pumping of fluids (both coelomic fluid and blood) into them. The external branchial muscle probably, as a result of its ventral origin, effects a depression of the whole funnel (as in text-fig. 3). The crossed fibres, no doubt, are responsible for the very wide opening of the funnel which is seen when the animal is fully expanded. One other small isolated

strand is connected with the branchiæ, and this also has a ventral origin. It accompanies the proximal part of the internal branchial nerve along the sides of the proboscis, as in text-fig. 20.

3. Of the muscles of the collar and thoracic membrane, one arises from a second, more ventral branch of the ventral longitudinal muscle. This lies beneath the subesophageal ganglion as far as the level of the second collar blood-vessel, then passes through the gland-shield into the base of the collar, and acts as an erector apparently (*M.e.c. 1*). A second erector (*M.e.c. 2*) lies immediately anterior to this, arising on the sheath of the subesophageal ganglion, and passing externally to the connectives into the base of the collar. A third strand (*M.e.c. 3*), much larger than these and lying mesially to them, takes origin dorsally at the level of the second transverse ciliated band, and passes obliquely antero-ventrally far into the collar.

At the level of the dorsal origin of the muscle are a few transverse fibres forming erectors of the collar-chætæ (*M.e.ch.tr.*), and the muscle *M.e.c. 3* in its origin surrounds these fibres (see text-fig. 14 B). The advantage of this arrangement is obvious. Both these fibres are erectors, and when they contract simultaneously the tone of the transverse fibres will make for the dorso-ventral fibres a firmer attachment than would the basement-membrane alone.

The chief erector of the dorsal angles of the collar is a strand which lies immediately lateral to the one just mentioned, and which takes its origin on the sheath of the subesophageal ganglion close to the origin of *M.e.c. 2*. It passes obliquely, laterally and anteriorly, against the anterior wall of the collar-parapodium, and finally enters the angle of the collar and spreads out in a fan-like manner over the whole of this region (*M.e.a. 1*). Other small intrinsic fibres, helping to stiffen the collar, occur laterally, and extend a short distance into the body-wall.

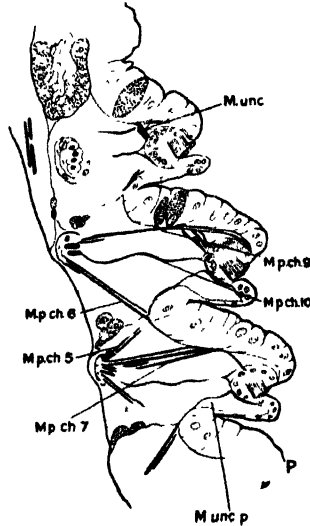
The reflexor (or depressor) musculature of the collar is much less elaborate. There is simply a dorso-ventral muscle (*M.d.c.*) arising in the head, partly in front of, and partly behind, the posterior ganglion: from here it goes ventrally, and is inserted in the collar among the terminations of the various erectors. The anterior half of this muscle slopes posteriorly ventrally, and hence is imagined to act as a depressor or reflexor; the posterior half, however, appears to be in a transverse plane, but has the ventral insertions diverging. This muscle does not seem to be sufficient to account for the reflexion of the collar round the opening of the tube, as it is seen when the animal is expanded. The only other suggestion which can be made to account for this is that the relative position of the various strands at the base of the collar forms the basis of control of the collar-movements. For instance, strands which pass into the collar near to the posterior (or external) edge, where it is thick and several cells across, will tend to contract this border and so reflect the membrane (see text-fig. 14 A).

All the muscle-fibres which have been named here are confined to the collar and to the anterior portion of the thoracic membrane: the hinder part of the membrane has no visible musculature, but it invests the parapodia so closely

that it is supported by the long notopodial chætæ, and is moved by the movements of them.

4. Lying against the parapodial walls in the thorax are certain fibres which are dorso-ventral in arrangement, but which curve dorsally so that they almost line the cavity. In continuity with these, mesially to the bases of the parapodia, are more fibres: they lie against the septa and hence are referred to as septal muscles (*M.s.* 1, 2, etc.). The strand immediately behind the collar-somite (*M.s.* 3) is rather larger than the rest, and the next one anterior to this between the collar-somite and the somite of the ring-vessel (*M.s.* 2) is very greatly enlarged. It forms a broad strand extending between the side-wall of the proboscis and the lateral body-wall, and originates dorsally behind the posterior ganglion of

TEXT-FIG. 16.



Three thoracic parapodia seen in horizontal section. Several consecutive sections are superimposed, and the anterior parapodium is shown at a more dorsal plane than the posterior one.

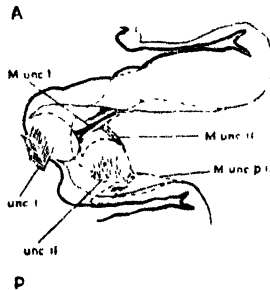
M.p.ch., protractor muscles of chætæ; *M.unc.*, retractor of uncini;
M.unc.p., accessory retractor of uncini; P., posterior.

the brain, lateral to the main dorsal strand. It runs posteriorly and ventrally down to the sub-oesophageal ganglion, and is continued backwards close to the ganglion, to be inserted in the body-wall immediately behind it. The first septal muscle (*M.s.* 1) lies at the back of the brain: it is not a complete partition, but is confined to the central region. In longitudinal sections this often appears to pass actually through the brain, and is described as doing so by some authors; but this is most probably a deceptive appearance, due to the curvature of the posterior surface of the brain at the sides of the muscle-fibres (see text-fig. 20).

There is still one other transverse strand, anterior to the last-mentioned, and hence prostomial in position: the fibres of this pass across dorso-ventrally from the head to the branchial base, at the lateral angles of, and immediately behind, the angle which separates these (text-figs. 19 & 20). In appearance this resembles the septal strands, but it has not been included in the septal series, as its homology is doubtful (*M.d.v.a.*): it lies in part between the two ganglia (or nerve-centres) of the brain, and if it were the case that these represented nerve-centres of two fused somites, then this muscle might well be the remnant of a septal fibre.

In the abdomen the septal fibres are so small that they are almost absent, but they are supplemented by oblique transcoelomic strands (*M.d.v.*), which are inserted ventrally on the body-wall at the level of the nerve-cords, and dorsally either among the fibres of the dorsal longitudinal muscle or against

TEXT-FIG. 17.



Camera-lucida drawings of two adjacent thoracic parapodia superimposed. For explanation, see text, p. 150.

A. & P. indicate anterior and posterior; *unc. i.*, uncinus of first somite; *M.unc. i.*, uncinal muscle of same somite; *unc. ii.*, uncinus of second somite; *M.unc. ii.*, corresponding muscle (contracted); *M.unc. p. ii.*, accessory retractor muscle of uncini of second somite (contracted).

the border of a parapodium. These dorso-ventral fibres are present also in the thorax, and it is probable that some of the collar-muscles are the enlarged anterior members of this series.

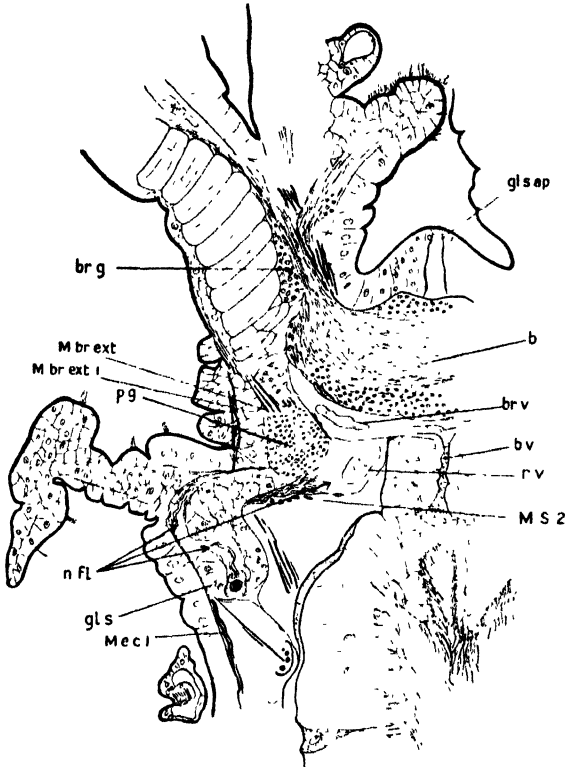
5. The chætal muscles include two independent sets, those of the long chætæ and those of the uncini.

The row of uncini is moved by a series of parallel muscle-fibres (*M.unc.*), one to each hook, arising on the anterior wall of the parapodium, in a transverse line parallel to the plane of the chætal sac, and inserted into the ridge which represents the sac. They appear both in life and in sections as single slender fibres, having a swelling near their insertion marking the position of the cell-nucleus.

When the animal is alive the uncini will sometimes keep up a rocking motion: the uncinal fibres effect the initial retraction of the uncini in this motion, but

the extreme retraction of the whole sac is effected by a slender fibre (*M.unc.p.*) inserted on the external and posterior margin of the uncinal lobe, and arising on the hind edge of the parapodial lobe. No set of fibres exists which could be antagonistic in their action to these retractors, hence some other mechanism must exist to bring about the return movement. The mechanism is probably produced by the passive spring-like action of the cells of the parapodial wall.

TEXT-FIG. 18.



Horizontal section (several consecutive sections combined) through prostomial and collar region, at a plane ventral to that figured in text-fig. 15.

Lettering as in text-fig. 14. In addition:—*b.*, brain; *gl. s.ap.*, aperture of excretory organ; *n.fl.*, nephrostomial flame; *r.v.*, ring-vessel.

The cells on the anterior wall are large and columnar, while the posterior face is formed by extremely thin flattened cells (text-figs. 12 & 16). When the uncinal fibres are in a state of contraction the curvature of the anterior face of the parapodium-wall will be increased, and the increase must exert a compression in these turgid cells. It may be that their elasticity causes sufficient resistance to this compression to cause the return of the uncini to their position of rest as soon as the muscle is relaxed. Text-fig. 17 shows the drawings of two

adjacent parapodia superimposed: one of these happened to be fixed with the uncinial fibres in a state of contraction (drawn with a dotted outline) and the other (with a plain outline) with the fibres relaxed. The effect of the contraction of the uncinial fibres on the anterior face of the parapodium is demonstrated in this way, and the appearance supports the suggestion given above as to the significance of the histological structure.

The long chætæ are moved by two sets of fibres—protractors and retractors. Of the former there are 10 strands, arising round the edge of (or at the apex of) the parapodium, and inserted into the bases of the two lobes of the chætal sac (text-fig. 16). Three of these arise dorsally in between the dorsal fibres and the basement of the epidermis (*M.p.ch.* 1-3). A fourth is ventral and short (*M.p.ch.* 4), arising in the region of the main longitudinal strand. Then there is an anterior strand, and a corresponding posterior strand (*M.p.ch.* 5 & 6) from the base, or rim, of the parapodial lobe, the posterior one of one segment arising just dorsally to the anterior one of the segment behind. There is a second anterior fibre arising on the wall of the lobe near its base, and a posterior one (dorsal) from the middle of the posterior wall of the lobe (*M.p.ch.* 7 & 8). There are also two long slender fibres arising at the apex of the lobe (*M.p.ch.* 9 & 10): the former is dorsal and arises in the angle between the anterior face of the uncinial sac and the parapodial wall, and the latter, more ventral, arises actually on the basement-membrane of the cells of the sac. These ten fibres are arranged to form a cone, though not a perfectly symmetrical one.

The retractors likewise form a cone (a more regular one) whose apex is formed by the mouth of the chætal sac, and whose base by the inner rim of the parapodial lobe (*M.r.ch.*). They are aided by a strand which passes from the base of the chætal sac down to the ventral body-wall at the level of the nerve-cords (*M.r.ch.p.*). This strand in the case of the collar-bristles can be traced through several somites.

All the muscles belonging to the collar-bristles are much larger than the corresponding muscles in the other somites. Owing to this fact, some fibres can be seen here which altogether escape notice in the other parapodia. However, having once found them in the large collar condition, indications of them can be observed in other places. Although it is practically certain that they are repeated all along the series, this is never very conclusively demonstrable. One of these (*M.e.ch.p.*) is the third dorsalmost branch of the main ventral muscle (text-fig. 14 A). It passes up the posterior face of the collar-parapodium, and is inserted on the posterior face of the chætal sac near its mouth: hence it will effect a posterior rotation of the bristles. The second is a transverse strand (*M.e.ch.tr.*): it is composed of two fibres and runs beneath the second transverse ciliated band at the back of the head. The two ends are inserted on to the two inner faces of the collar chætal sacs: hence it will serve to approximate them, and thus to raise the angles of the collar itself.

The first of these two muscles is probably antagonistic to the retractor (*M.r.ch.p.*). It is supposed that the animal moves in and out of its tube by

levering itself on its chaetae—no other method would appear to be sufficiently rapid to account for the instantaneous disappearance of the creature into the tube when disturbed. If so, then the action of the muscles of the series corresponding to *M.e.ch.p.* would protrude the body, and the more powerful *M.r.ch.p.* series would effect the return into the tube.

5. The alimentary canal is invested with a sheath of circular muscle-fibres between the hind end of the achæitous zone and the tip of the proboscis, lying external to the peri-enteric sinus. These are responsible for the anti-peristaltic contractions, which sometimes pass over this region (text-figs. 20 & 22).

Although the muscles in this description have been grouped according to function, they would fit equally easily into a scheme based on homology, since they are all probably to be regarded simply as somewhat modified members of a metameric series.

3. Central Nervous System.

The nervous system throughout its course is in close contact with the epidermis: it is not clearly separated off from this, and the ganglion-cells lie among the bases of the epidermal cells. The fibrous cords themselves lie also among the epidermal cells in the posterior part of the abdomen, and the branchial nerves have a similar position. The two halves of the cord are widely separated and connected by commissures, so that a typical ladder-like arrangement results. The peri-oesophageal connectives are short and broad, connecting the sub-oesophageal ganglia with the postero-lateral regions of the brain.

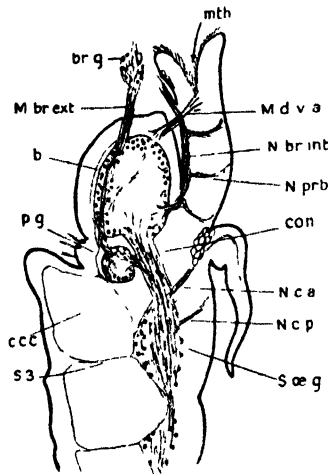
The brain occupies almost the entire cavity of the head (see text-figs. 2, 22, 26, etc.). The nerve-cells are restricted to the periphery, and the arrangement both of these and also of the fibres suggests that there are two pairs of ganglia or nerve-centres in the cerebral mass. An additional pair of ganglia, the posterior cerebral ganglia (*p.c.g.*), lies immediately behind the brain. It is usual for the brain of Polychætes to show three pairs of ganglia (for bibliography of this subject, see Fortuyn, 1920), but in this case the third pair is separate from the other two: hence the concentration of nerve-centres is less here than in the free-living forms. In other Polychætes this third ganglion supplies the nuchal organ: in this case it is in very close contact with the cells of the first transverse band of cilia; but with the methods which up to the present have been employed, it is not possible to state definitely whether or not there is a fibrous connection between the two. The detailed histology of this and of other points has not been undertaken, as it was considered to be too large a subject to deal with in a general paper: hence only the general anatomical features are described here.

The sub-oesophageal ganglia are merely the enlarged ganglia of the collar somite. They are followed by a series of comparable smaller ganglia in the other thoracic somites. In the abdomen the cords have smaller ganglionic swellings; they taper gradually and terminate in the anal papillæ.

Cerebral nerves:—There are two pairs of nerves issuing from the brain to

supply the branchiæ. One leaves at the antero-lateral angles of the brain (*N.br.ext.*) and passes into the branchial base, where it bears a ganglionic swelling (see text-figs. 14, 18, & 19). From this, branches arise to supply the tentacle and the external faces of the branchial axes. Two of these external strands pass up each axis (text-fig. 4 A): at the base, however, the adjacent strands of neighbouring filaments are confluent, so that there are at first five, and finally eight of these strands on each side. For the first part of their course they lie against the basement-membrane of the external wall of the filament, but almost at once they insert themselves between the cells, and come to lie close against the cuticle. They give a branch into each pinnule.

TEXT-FIG. 19.



Diagrammatic lateral view of prostomium and proboscis, to show the brain and branchial nerves.

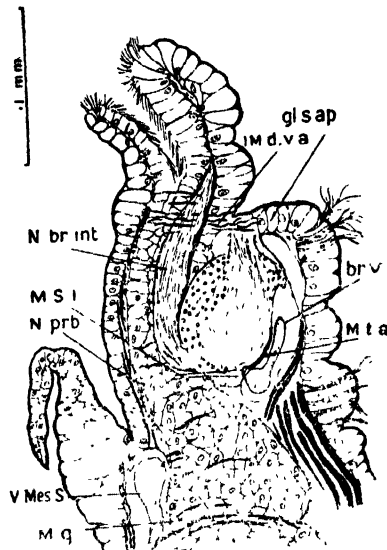
b, brain; *brg*, branchial ganglion; *c.c.c.*, coelomic cavity of collar-somite; *con.*, pericardial connectives; *M.d.v.a.*, anterior dorsal-ventral strand; *M.br.ext.* (should be *N.br.ext.*), external branchial nerve; *mth.*, mouth; *N.br.int.*, internal branchial nerve; *N.c.a.*, anterior collar-nerve; *N.c.p.*, posterior collar-nerve; *N.pr.b.*, nerve-rings round proboscis; *s.3*, third septal muscle; *s.o.g.*, sub-oesophageal ganglion.

The second branchial nerve (text-figs. 19 & 20) leaves the brain at its hind end, ventrally, and near the middle line. This nerve in the first part of its course is closely applied to the proboscis and provides the nerve-supply for this. After leaving the brain the nerve turns forwards and runs along the sides of the proboscis, giving off at intervals branches which encircle this: when close to the mouth it enters the branchial base, and almost at once divides into four. One branch enters each filament, lying on the mesial side of the axis and in its middle line (see text-figs. 4, A & B). It lies inside the epidermis against its basement-membrane, and is referred to as the internal branchial nerve

(*N.br.int.*). During its course up the axis it gives off a double series of lateral branches to the pinnules: these are extremely fine and are seen in longitudinal sections only.

The fibres composing the internal branchial nerve arise in the hind part of the brain, but those which form the external nerve, though they issue from the anterior end of the brain, can be traced to a more posterior origin. They pass posteriorly through the dorsal part of the brain into the posterior cerebral ganglia. Hence in their origin, as well as in their final disposition in the branchiæ, they are posterior to the internal nerves.

TEXT-FIG. 20.



Longitudinal section (not median) of prostomium and proboscis, to show relationships between nervous system, blood-vessels, and musculature.

br.v., branchial vessel; *gl.s.ap.*, aperture of excretory organ; *M.d.v.a.*, anterior dorso-ventral strand; *M.g.*, circular muscles of gut; *M.s.l.*, muscle-fibres in first septum; *M.t.a.*, anterior transverse fibres; *N.br.int.*, internal branchial nerve; *N.pr.b.*, nerve-ring round proboscis; *v.mes.s.*, ventral mesenteric sinus.

Sections cut sagittally (as text-fig. 14 B) show further that fibres from the posterior ganglia take part in the formation of the peri-oesophageal connectives: they unite with the main bundle soon after it leaves the hind end of the cerebral mass.

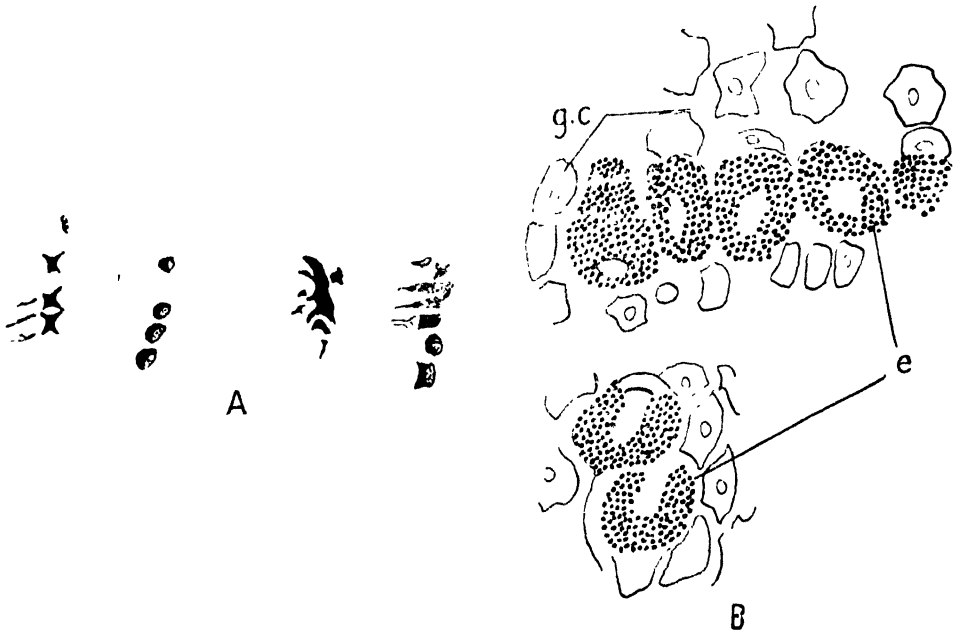
Arising from the sub-oesophageal ganglia are two pairs of nerves which supply the collar and thoracic membrane. The more anterior (*N.c.a.*) arises at the level of union of connective and ganglion, and passes forwards close to, and parallel to, the muscle *M.e.c. 2*. It lies between the two layers of cells forming the collar (text-figs. 14, 19, & 26). The more posterior (*N.c.p.*) arises in the

same transverse plane as the commissure and passes laterally into the membrane, lying adjacent to the posterior blood-vessel of the collar, and externally to the glandular sac.

The nerves arising from the posterior ganglia are extremely small, but at least one pair can be found in each somite and traced as far as the base of the parapodium.

Of the previous authors writing on the nervous system, Treadwell (1891) describes the internal and external nerves in the branchial filaments, but states that they arise by bifurcation of a single nerve each side.

TEXT-FIG. 21.



A. External appearance of the row of eyes of four individuals.

B. The eyes seen in transverse section.

e., eye, the pigmented cup; g c., ganglion-cells of brain.

It is of considerable interest to note also that Eisig (1887), in his monograph on Capitellidæ, describes some genera as having posterior ganglia incompletely incorporated into the cerebral mass just as in *Filograna*, e. g., *Mastobranchus*.

SENSE-ORGANS.

The eyes (see p. 116), when seen in section, are found to be situated in the interior of the brain near its ventral side: each is composed of a hollow cup of pigment-globules (text-fig. 21), situated within an enlarged cell, whose nucleus lies at the foot of the cup.

The nuchal organ of Polychætes is a structure which is extremely variable both in size and form, and its homology in Serpulids has not previously been decided with certainty. The most useful diagnosis depends on the fact that it is innervated from the third cerebral ganglion—the posterior cerebral ganglion of *Filograna*. As stated above, this ganglion is in close contact with the cells of the first transverse ciliated band, and, though a nervous connection between the two has not been demonstrated, yet it seems probable that the band may represent the nuchal organ. According to Racovitza (1896), the organ “n'est que la spécialisation d'un point de la surface sensitive,” and, further, he states that at its simplest, it has “l'état primitif d'aire sensible.” Such a description would apply to the localised specialisation of the epidermal cells as seen in *Filograna*. Meyer (1888) states that the unpaired terminal portion of the ciliated duct of the excretory sac is innervated by the nuchal nerves, and he upholds (as does also Pruvot, 1895) that this is the homologue of the nuchal organ. No evidence has been found for this view, and in any case the particular part of the excretory canal referred to is the one place where it is not ciliated, and hence it lacks the most characteristic feature of a nuchal organ.

A structure which is presumed to be a variety of oral sense-organ is found on the dorsal lip of the proboscis, near its tip: it consists of a large clear projecting cell (one on each side of the middle line), and is supplied by a comparatively large nerve-strand arising from the internal branchial nerve near its base where it is lying against the proboscis.

The palpcils are probably sensory in function, but no special observations have been made on them.

BLOOD-SYSTEM.

The blood of *Filograna* is a homogeneous fluid having a green colour, due to the presence of the pigment chlorocruorin. It is devoid of corpuscles; the cells, which have been described as lying in the blood-sinus, are probably cells which are crossing the cavity in order to reach the wall of the alimentary canal, where they are required to replace cells which are being discarded during the process of degeneration.

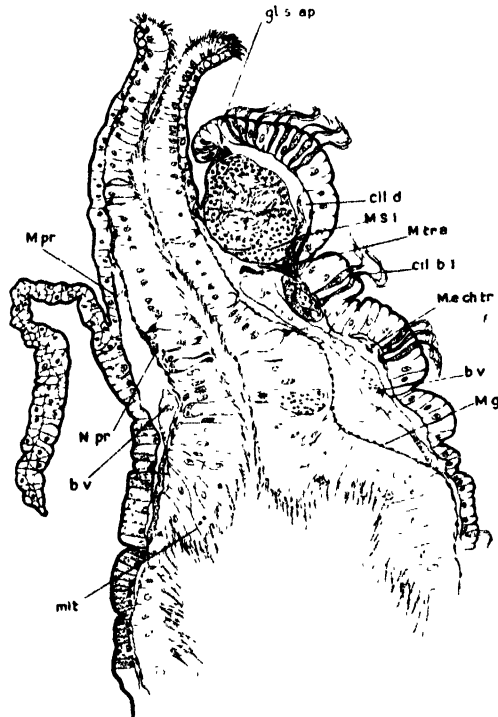
The blood lies for the most part distributed in broad sinusoid spaces: it is thus practically unconfined and cannot have any true circulatory movement. Such movement as does occur is due to pressure exerted on the sinuses by muscular movements of the body, or of other organs (*e. g.*, the anti-peristaltic movements of the gut), and is aided no doubt by the extensibility and elasticity of the protoplasmic (non-muscular) walls of the sinuses. Fuchs (1907) and Meyer (1888) both state that most of the vessels in Serpulids are contractile, and Fuchs mentions the pulsation of terminal ampullæ on them, but this is not the case in *Filograna*. The only visible fibres which are in contact with any part of the blood-system are the circular fibres which surround the perienteric sinus in the thoracic and in the achæitous zones.

The distribution of these sinuses is identical with that of the cavities (normally

only virtually cavities), which may be described as blastocœlic : hence they are entirely outside the cœlom and lie, in fact, between it and the adjacent organs or tissues.

The main sinus surrounds the gut from the anus to the level of the junction between the proboscis and thoracic gut, at the hind end of the collar-somite (text-figs. 2, 15, etc.). It is one uninterrupted space, crossed, however, at

TEXT-FIG. 22.



Median longitudinal section through prostomium and proboscis.

b.v., blood-vessels, parts of anterior ring; *cil.d.*, ciliated duct of excretory organ; *cil.b.*, first transverse ciliated band; *gl.s.ap.*, aperture of excretory organ; *M.e.ch.tr.*, transverse erector muscle of collar-chaeta; *M.g.*, circular muscles of gut; *M.pr.*, proboscis-muscle; *M.s.l.*, muscle-fibres in first septum; *M.tr.a.*, anterior transverse fibres; *mit.*, mitosis in epithelium of gut; *N.pr.*, nerve-ring round proboscis.

intervals by extremely thin protoplasmic strands of tissue stretching between the gut-epithelium and the peritoneum. The blood in the sinuses spreads into the dorsal and ventral mesenteries between the two layers of epithelium, and, generally, that which lies in the ventral mesentery is restricted to the ventral-most part of it, producing here a canal resembling a longitudinal vessel: it is, however, not surrounded by any wall other than the covering of peritoneum. Similarly, the blood penetrates into the space between the two halves of each

dissepiment ; but again, instead of being distributed evenly over the available area, is confined to the superficial margin of the septum, and so appears as a ring-shaped commissure connecting the sinuses in the dorsal and ventral mesenteries. Here, also, there is no intrinsic wall, but only a covering of peritoneal epithelium. This epithelium is sometimes, particularly in the genital segments, produced into a backwardly pointing caecum, which is filled with blood and hangs freely in the body-cavity at the base of the parapodium, ending blindly. Often, also, there is a smaller swelling of the sinus on the walls of the dissepiment, producing a small pouch : this becomes covered with a mass of granular cells, which are distinct from the peritoneal cells, as they are much larger and contain in their protoplasm an irregularly shaped mass having a refringent yellowish appearance (text-fig. 24). These are probably of the nature of chloragogen-cells and agree with the description of similar cell-aggregates given by Winterstein (1925).

Further, there is a thin sub-epidermal sinus : this is most marked in the region of the nerve-cords, and forms a distinct canal accompanying these on their internal aspects. It is doubtful whether this sub-epidermal sinus is universally present. It is in all cases so thin that it is not seen, except with the aid of special methods (as described below), and it can be seen with certainty only in those parts of the body-wall where the somatic peritoneum lies close to the epidermis. Where it is widely separated by the intervention of longitudinal muscles, and the "blastocoelic" space is correspondingly enlarged, the sinus seems to be non-existent.

Anteriorly the sinuses become restricted : they are confined within definite tubular channels, which may strictly be described as vessels. Their walls are extremely delicate, being formed by a layer of very flat membranous epithelial cells, identical with those of the peritoneum covering the sinuses. No doubt, these vessels are to be considered as channels which have been derived by the closure and subsequent pinching off of grooves along the walls of the sinuses. Although the development of the vessel has not been followed, there is some evidence for this to be found in the method of formation of the anterior vessels in the bud (see below, p. 163).

At the base of the proboscis the peri-enteric sinus ends, and its cavity is continued forwards in a median dorsal vessel. This bifurcates posterior to the brain, immediately beneath the first transverse ciliated band (text-figs. 2, 15, 18, 20, 22), and the branches at first pass outwards, then obliquely ventrally and posteriorly round the proboscis. Finally, the two unite with the ventral mesenteric sinus at the back of the collar somite : a complete ring is thus formed, lodged almost entirely within the pre-collar somite.

At the dorso-lateral angles of this ring a branchial vessel is given off on each side : this passes above the brain into the branchial base, where it divides into four. Each branch enters a filament and sends a lateral branch into each pinnule. These, together with the main axial vessel, end blindly.

From the ring-vessel two other pairs of branches are given off (text-fig. 2)

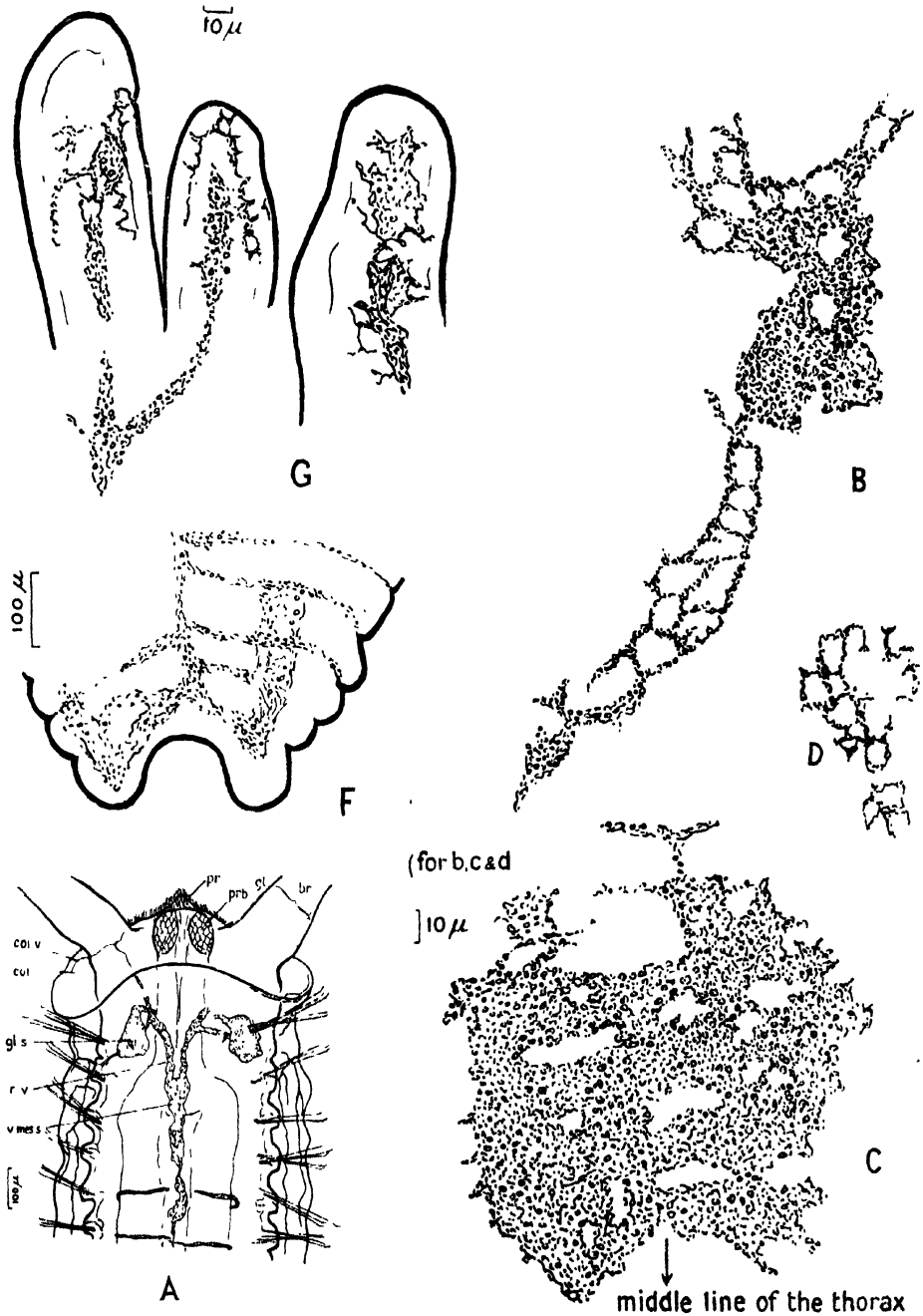
to supply the thoracic membrane. The more anterior one lies parallel with the anterior collar-nerve and the muscle (*M.e.c.* 2), and enters the base of the collar; the other is more ventral and posterior, and runs transversely beneath the sub-intestinal ganglion, then turns dorsally and enters the thoracic membrane. It subdivides into several branches, some of which pass to the hind end of the membrane. The number and pattern of these are not constant: they have a sinuous course, and finally end blindly; in the membrane they lie between the two layers of cells composing it.

When any particular sinus is examined in several series of sections it is noticed that there is great variability in the amount of blood present in the different cases: this may be taken to demonstrate the fact that transport of the fluid does actually occur in a simple system such as this. Further, the amount of blood present in any particular region seems to vary considerably with the state of activity of the animal. In a budding animal, for example, the sinuses in the posterior somites are greatly enlarged; in a similar manner, too, the posterior tip of a non-budding individual, *i. e.*, the actively growing region, often appears green from the exterior, owing to the enlargement of its blood-sinuses. It is chiefly, though not entirely, the peri-enteric sinus which shows this enlargement. At the level of the anus, where there is a transition from ectoderm to endoderm, there is a corresponding transition between the spacious sub-endodermal sinus and the more restricted sub-epidermal sinuses. Although the change from ectoderm to endoderm is abrupt, the sinuses change their character more gradually, and there may be a quite extensive sub-epidermal sinus here, large enough to give a green tint to the tip. Further, it seems that there occurs in the hind two or three segments an extravasation of blood from the sinuses into the coelomic cavities: the appearances of both living and sectioned animals indicates this.

The observation of the finer details of this system have been aided by the application of a common chemical test for blood-pigments (*i. e.*, peroxydases) to the living animal. The method is described by Romieu (1922), but is given by him as a method for staining the Annelid nerve-cord. Romieu states that the action depends upon the presence of hæmoglobin in the nerve-cord; in the case of *Filigrana*, however, the nerve-cord is unaffected, but, on the other hand, the superficial portions of the blood-system (and sometimes the deeper portions also) showed the reaction beautifully. The small size and the transparency of the animal allow the details to be examined in the living under a high magnification, even under a $\frac{1}{16}$ -in. oil immersion lens.

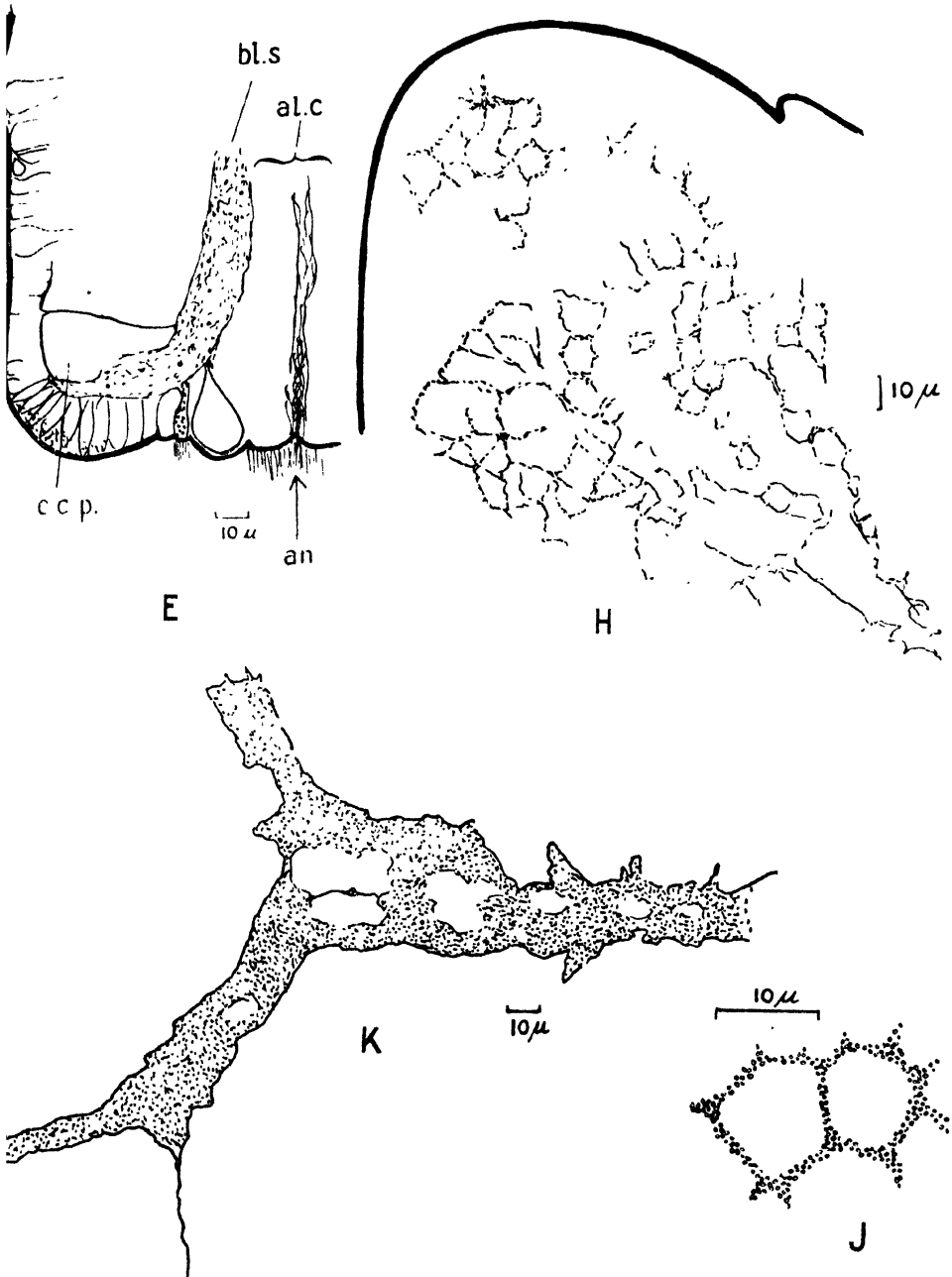
The method employed was as follows. A solution of benzidene was obtained by sprinkling a little of the substance on sea-water, and leaving for half an hour or more. The substance is very slightly soluble, but a dilute solution is what is required. The sea-water is filtered and the *Filigrana* immersed in it for a period varying from a quarter of an hour to two hours. They are then transferred to pure sea-water, and hydrogen peroxide is added drop by drop. When small bubbles of gas appear, enough has been added: the blood then begins to

TEXT-FIG 23.



Camera-lucida drawings from living animals of blood-sinuses after treatment with the benzidene-hydrogen peroxide method. For explanation, see text, p. 162.

- A. Ventral view of thorax. B. Portion of ventral vessel in thorax. C. Portion of mid-dorsal body-wall, immediately posterior to hind end of proboscis. D. Honeycomb of small size, in ventral edge of collar. E. Anal region, to show termination of peri-enteric sinus (unstained animal). F. Same region as E, stained with benzidene.

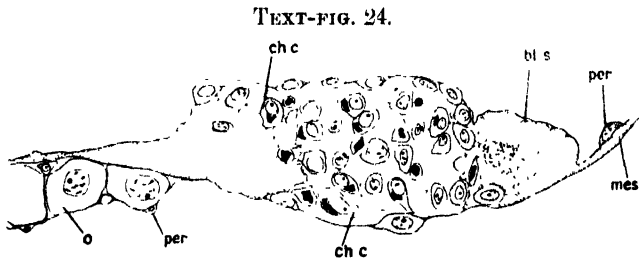


G. Branchiæ of bud, showing superficial (sub-epidermal) network in continuity with branchial vessel. H. A specially good honeycomb on the branchiæ of a bud (under $\frac{1}{8}$ -in. objective). J. A few cells of the same under a $\frac{1}{8}$ -in. oil immersion lens. K. Bifurcation of dorsal vessel in bud. (Left is anterior.)

al.c., alimentary canal; *br.*, branchiæ; *gl.s.*, glandular sac; *pr.b.gl.*, proboscis-land; *v.r.*, ring-vessel; *bl.*, blood-sinus; *c.c.p.*, posterior coelomic cavity; *col.*, collar; *pr.*, prostomium; *col.v.*, collar-vessel; *v.mes.s.*, ventral sinus.

show as dark blue patches. Under varying experimental conditions different portions of the blood-system reacted, and by examining a large number of individuals the whole was made out. Text-figure 23, A-K, was drawn with the aid of a Leitz Zeichen-Okular from animals treated in this way. The shaded areas represent the blue-stained blood; the colour is deposited as granules or small discs, and sometimes in the larger spaces as long needle-shaped crystals lying in bundles or stars.

The sinusoid nature of all except the anterior vessels is convincingly demonstrated, and the results confirm the conclusions drawn from other observations. But the most valuable results obtained are those concerning the sub-epidermal sinuses. These are so small that they are generally invisible in sections, and in life, though visible, are so pale that their appearance is not really conclusive. They are seen only under a high magnification (*e. g.*, $\frac{1}{16}$ -in. obj.), and their pale green colour might be an optical effect; but when stained with Prussian blue there is no doubt as to their presence or their nature.



Horizontal section of a blood-sinus on an abdominal dissepiment, to show the enlargement of the blood-space and chloragogen-cells.

bl.s., blood-sinus; *ch.c.*, chloragogen-cells; *mes.*, dissepiment; *o.*, oocyte; *per.*, peritoneal cells.

The ventral mesenteric vessels and the commissural vessels are generally seen, and the ventral portion of the anterior ring (text-fig. 23, A); the dorsal part, being less superficial, does not stain well, except in buds. The sub-epidermal sinus is seen in patches: one squarish patch constantly appears on the anterior third of the thorax dorsally, and (not quite so constantly) another on the hind thoracic and achæitous zone. There is never a trace of blue in the one place where the sinus is enlarged and one would therefore expect it, namely, along the neural sinuses: this may be due to the fact that the nerve-cord itself makes a thick impenetrable ridge in the body-wall, which the reagents do not pass through.

The appearance of the sub-epidermal sinus varies somewhat. Sometimes it is a broad expanse of blue; at other times clear transparent patches are left standing out against a blue background (text-fig. 23, C). Such spaces correspond exactly in size, position, and shape to one or other of the types of epidermal cells observed under other conditions: very frequently the form of the spaces

coincides with that of the clear lobed cells filled with globules as described in the paragraph on the anal glandular patch. The appearance suggests that these large swollen cells obliterate the cavity of the sinus, and so are indicated as colourless areas. In still other places the blue is reduced to a mere honeycomb, precisely similar to the pale green network which is seen in a normal untreated animal. The size of the mesh of the honeycomb varies in different parts of the body, and is evidently to be regarded as outlining the epithelial cells, as the size varies in correspondence with the variation of these cells (text-fig. 23, D).

Sometimes the peri-enteric sinus is stained also, but this is easily distinguished from the superficial sinus by focussing the microscope.

The appearance of the main mesenteric "vessels" is interesting, too, as it emphasises the fact that they are not simple tubular canals, but open spaces. The median strand of blood fades away laterally quite irregularly, generally in a series of pointed projections, which may be regarded as inter-cellular processes, and often clear cellular areas are left unstained in the middle of the vessel, as described above as happening in the expanses of the sub-epidermal sinuses. Text-fig. 23, B, shows a portion of the ventral sinus in which one half is fairly full of blood and the other much less full, and showing the honeycomb form rather than the typical canal.

The communication between the sub-epidermal sinuses and the larger sinusoid vessels is demonstrated by this method much more plainly than by the use of serial sections. The condition in the case of the mesenteric vessels has just been described: another case is provided in the anal region. Here, as in text-fig. 23, E & F, the continuity between the two is obvious. Further than that, a similar condition is exhibited in the developing vessels of the head of a bud. Text-figure 23, G & H, shows the branchial filaments of a young bud: the branching of the main branchial vessels is shown, and the passage of the branches into the bases of the branchiæ. Here, however, instead of the simple finger-shaped blind terminations that are seen in older buds or adults, the vessel fades away among the blood of the sub-epidermal region. This, together with the appearance of figure 23, K, shows that the blood-vessels of the bud are formed by the restriction and enclosure of the wider sinusoid expanses of the stock. Text-figure 23, H, shows the formation of the anterior ring-vessel of the bud. The median vessel of the stock is apparently being obliterated at the point of bifurcation. Similarly, in the branchiæ it seems that an enlarged portion of the sub-epidermal sinus becomes separated off as the vessel. (The course of events in the larva has not been followed.)

This type of blood-system is practically the simplest conceivable for an Annelid—whether it is equally primitive is not so easy to say. The question of the probable origin of, and the evolution of, the blood-system in Annelids has been discussed fully by Stephenson (1913), and, according to his theory, the spacious peri-enteric sinuses of Serpulids have been derived secondarily from a network of vessels and sinuses, such as occur in the genus *Æolosoma*,

by spreading and fusion of the separate lacunæ. Lang (1904), on the other hand, considers that the primitive Annelid possessed a system almost identical with that just described, formed of a gut-sinus lying between the gut-wall and the peritoneum, with septal and mesenteric sinuses communicating with it. Eugen Lee (1912) supports Lang's theory entirely, and emphasises the fact that this theory of the origin of the blood-spaces in Annelids accounts for the fact that the vessels have no intrinsic epithelial lining. The embryological evidence of Giard (1876) working on *Salmacina*, and of Selensky (1882) on *Psygmorebranchus*, all confirms this suggestion, for they describe the blood-cavity as arising by a separation of the already adjacent epithelia of the gut and of the splanchnic peritoneum.

The condition resulting from this process is precisely what is found in the adult *Filograna*, and the complete absence of any trace of walls (apart from the peritoneum) is quite certain in this case. The various authors writing on this subject are not unanimous in deciding whether the blood-vessels of Annelids have, or have not, an endothelial lining*. The most recent paper (Federighi, 1928) states that some of the vessels do possess an endothelium and that some do not. In support of the negative statement, Dyrssen (1912) states definitely that in *Cirratulus* there is no vaso-endothelium, but that "die innere Gefäßmembran nur eine Fortsetzung der Grundmembran des Dissepimentes darstellt."

This theory is supported and extended by de Beauchamp (1911). According to this author, the cavity of the blood-system may be considered as a blastocœl. Lang denies this, in spite of the fact that his figures and descriptions emphasise the similarity in the distribution of the two. De Beauchamp defines a blastocœl as any cavity which separates any two of the primary cell-layers, as distinguished from cavities which are comprised within one of them. Hence he considers that the cavity of the blood-system is theoretically a blastocœlic space "même si elle s'oblitére avant de se reformer au cours du développement." The exact correspondence between the two series of spaces in the adult *Filograna* strongly supports this view, and a diagram which de Beauchamp gives (fig. 7) as a schematic representation of a primitive condition could be taken to apply to *Filograna*.

The blood-fluid is distributed in *Filograna* in a manner similar to that in which it is distributed in forms provided with vessels and capillaries, but whether the absence of these is a case of primitive or of secondarily acquired simplicity it is difficult to say.

Concerning the origin of the blood-fluid itself, Stephenson regards it as an accumulation of fluid diffused through the gut-walls from the enteron and containing dissolved in it food-substances, mineral matters, and oxygen. Lang, Lee, and Vejdosky (1905) are all agreed in assuming that the blood was primarily a nutritive fluid, and that the peri-enteric spaces are the most primitive portions

* Meyer (1901) stated that the presence of an intima in the vessels of Annelids had not been proved, and that he definitely thought it was absent.

of the system : this last point does not hold if the blastocoelic hypothesis is correct.

In the most primitive Annelids there was probably a gut surrounded with coelomic sacs, and hence possessing a double wall. The cavity between the two layers of the wall is theoretically blastocœl, and, in that case, if the cavity is still existent at that stage of development (or evolution) at which blood first appears, would already be filled with some kind of fluid. Further, this fluid would from the first be widely distributed, and of the nature of a ready-made medium of communication between the cells of the body. If dissolved food-matters were secreted into it from the gut they would diffuse by simple physical processes throughout its whole extent, and the diffusion would be aided by movements.

The difference between this view and those quoted above is that the latter regard the blood-system as something arising *de novo*, for nutritive purposes primarily, whereas the former assumes rather the adaptation of a pre-existing body-fluid, and takes into account both the adaptation to food-transport and to respiration.

It is deduced from most of the authors mentioned above that the formation of external respiratory organs was something superimposed on the blood-system after it had acquired its last-formed portion—namely, the peripheral (this is presuming that respiration was a surface activity). It is difficult to imagine a second function being developed after the first (*i. e.*, food-carrying) was so well established, and if it be assumed that the blastocoelic fluid is the original basis of the blood the difficulty does not arise. For at the very earliest stages the peripheral parts are developed to the same extent as the enteric, and the two functions can be imagined to have arisen simultaneously.

The suggestion that the blood is derived from the blastocoelic fluid accords with the theories of Macallum concerning body-fluids. He assumes (1926) that the blood of primitive animals was merely a duplication, chemically and physically, of the external medium on which these animals lived, namely, the primitive sea-water. This is imagined to have passed by some means into the internal cavities of the creatures, and obviously, if this were so, the water which passed in would find itself in the blastocœl.

According to this hypothesis, the vessels of other less simple Annelids are imagined to be derived by restriction of the sinusoid spaces to circular channels, as happens anteriorly in *Filigrana*. The precise origin of the complex thick walls of these cannot be guessed from the particular genus under discussion. However, a hint is supplied which may help to account for the difference in musculature between the dorsal and the ventral vessels. *Filigrana* agrees with the general rule laid down for Annelids, that the differentiation of the ventral vessel is in advance of that of the dorsal. The ventral one shows a fairly precise circular outline, whereas the dorsal is more in the nature of a vague swelling, spreading all over the mesentery : further, the ventral is more detached from the gut, and hence is removed from contact with the gut-muscles. It is concluded

from this that if a vessel originates in a mesentery near its external (dorsal or ventral) attachment, or if it originates in the gut but separates from this before the musculature is developed, then the vessel would be expected to be non-muscular; on the other hand, if it does not become separated till after the gut-muscles are formed, then it is probable that it would retain the muscular coat, as it does in the dorsal vessel of most Annelids.

This particular blood-system, with its anterior concentration of vessels, is adapted to the tubicolous habit of the animal. The blood is forced into the so-called branchiæ by the action of the thoracic gut-muscles. Anti-peristaltic waves are seen to pass over this region, and the effect of these is probably reinforced by a simultaneous contraction of the circular muscles, which are present in the body-wall in the achæitous zone. The expansion of the branchiæ thus effected provides the mechanism for the capture of food.

CŒLOMIC CAVITIES.

The cœlom in the abdominal region is a fairly spacious cavity, except at the time when the genital products are mature, but in the thorax it is greatly reduced as a result of the enlargement of the gut. It is divided into chambers from the head to the anus, longitudinally by the dorsal and ventral mesenteries supporting the gut, and transversely by the dissepiments between the segments. In the abdomen, therefore, the cavities are simple rings. In the thorax, though the cavity is reduced, it is still obvious, but in the achæitous zone the walls of the gut are pressed against the body-wall so that the cœlom is almost obliterated. However, the septa can still be distinguished (text-fig. 5, H).

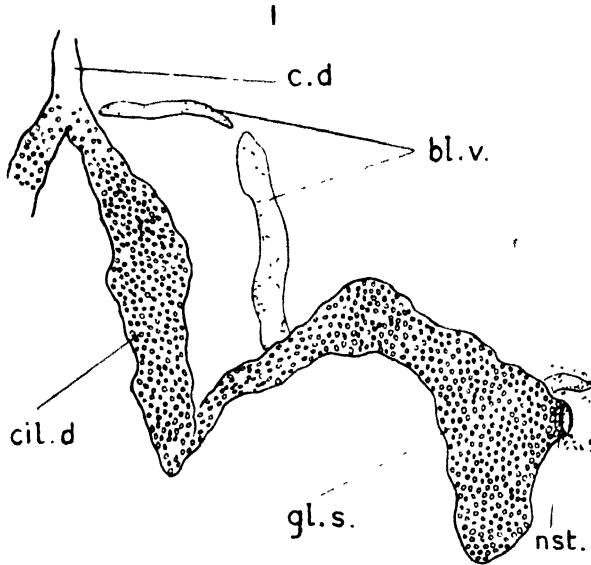
The cœlomic epithelium is extremely thin, but is rendered conspicuous by the fact that there are blood-sinuses separating the two halves of the double mesenteries and underlying the splanchnic layer. The epithelium is membranous and bears at intervals small swellings which indicate the position of the cell-nuclei. In the sexual somites at the time of maturity, the cells lining the tubular genital duct and those of the epithelium round its inner opening become ciliated.

The most anterior somites are somewhat modified in size and form. The collar-cavity is larger than any other. It surrounds the gut where this is at its narrowest, *i. e.*, in the proboscis-region; further, it possesses a pouch-like prolongation extending backwards between the gut and the cœlomic cavities of the one or two succeeding somites, and lodging the collar-chætæ when these are retracted (text-figs. 15 & 26). The somite anterior to this, the pre-collar somite, lodges the blood-ring and the branchial vessels. A dorso-lateral outgrowth on each side enters the branchial base (text-figs. 18 & 26), and subdivides to send a branch up each of the four filaments. These in turn send branches into the pinnules. These branches lodge a precisely similar system of blood-vessels, which arise from the lateral angles of the collar-ring. There is another outgrowth from the pre-collar cavity (the nephrostomial tube), for a description of which see the section on "Excretory Organs."

GLANDULAR SAC AND EXCRETION.

Filograna agrees with other tubicolous Annelids in having its excretory organs confined to the anterior somites (Meisenheimer, 1909): these are situated at the anterior end; in the more posterior segments, the only communications which can be found between the coelom and the exterior are the ciliated gonoducts in the genital segments. There is one pair of anterior excretory organs in the form of a pair of ciliated tubes whose inner ends are swollen into sac-like pigmented bodies (the glandular sacs) and whose distal ends unite to form a common terminal duct (text-figs. 2, 14, 15, 18, 25, & 26).

TEXT-FIG. 25.



One of the two glandular sacs, as seen in life in a particularly favourable individual, showing the nephrostomal opening.

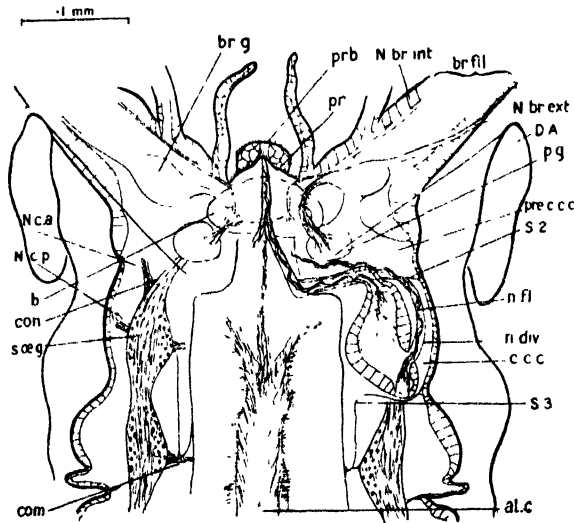
bl. v., blood-vessel; *c. d.*, common duct of the two sacs; *cil. d.*, ciliated duct; *gl. s.*, glandular sac; *nst.*, nephrostome.

The sacs lie at the sides of the collar-somite against the lateral body-wall, dorsal to the nerve-ganglion. At its anterior end the sac narrows to form a tubular duct, which throughout its course lies close against the dorsal epidermis. It bends inwards almost at once at a right angle, and when near the middle line turns forwards by another right angle. At the back of the head the tubes from the two sides unite and a common median duct continues forwards dorsal to the brain to the tip of the prostomium, where it opens on a pore situated on a small median papilla and guarded by several large pear-shaped cells (text-fig. 22). The organs are said to be the persistent protonephridia of the larva by Meyer (1888) and Malaquin (1908). The walls of the duct (which is intercellular), as seen in section, are not of equal thickness all round: they are thick on the side adjacent to the coelomic cavity and thin externally (text-fig. 15).

The sac and the duct, with the exception of the common terminal part, have their cells filled with greenish granules. Also they both are ciliated, the cilia being so long in the duct that they appear in the living animal to form a flame, following the bends of the tube, and reaching almost to the pore. The beating of this flame keeps the granules constantly vibrating.

The so-called sac is not a closed vesicle, but communicates through a pore in its outer wall with the coelom of the pre-collar somite (text-fig. 26). It agrees

TEXT-FIG. 26.



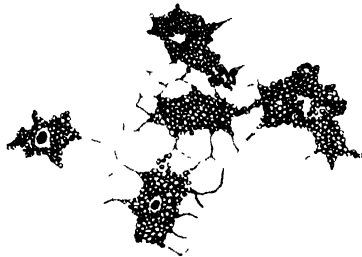
Diagrammatic representation of the anterior end in horizontal view, to show relationships between glandular sac and coelomic cavities; also nervous system and alimentary canal.

al.c., alimentary canal; *b.*, brain; *br.g.*, branchial ganglion; *br.fil.*, branchial filament; *c.c.c.*, coelom of collar-somite; *com.*, nerve-commissure; *con.*, peri-oesophageal connectives; *D.A.*, dorsal angle of collar; *N.br.ext.*, external branchial nerve; *N.br.int.*, internal branchial nerve; *N.c.a.*, anterior collar-nerve; *N.c.p.*, posterior collar-nerve; *n.dir.*, nephrostomial diverticulum; *n.fl.*, nephrostomial flame; *p.g.*, posterior cerebral ganglion; *pr.*, proboscis; *pre.c.c.*, coelom of pre-collar somite; *prb.*, proboscis; *s.*, dissepiment; *s.a.g.*, sub-oesophageal ganglion.

thus with the nephridia of other Serpulids, as described by Meyer (1888) and Lee (1912), although in the case of *Filograna* neither Lee nor Malaquin (1908) could find the aperture of the sac. The hind wall of this somite is produced into a long tubular (or funnel-shaped) diverticulum, which inserts itself between the sub-oesophageal ganglion and the glandular sac (text-fig. 18), and which lies just within the lateral body-wall in the region of the muscle (*M.br.ext.* 1). The pore of the glandular sac opens into the base of this tube; hence it has the characters of an open nephrostome, being, however, somewhat peculiar in the

disposition of the cilia connected with it. At the hind end of the sac is a large posterior cell, from which a group of very large cilia arise. These pass through the pore, beat up the nephrostomial tube towards its mouth, and extend into and across the main cavity of the pre-collar somite; the length of this flame-like structure is $200\ \mu$ ($\cdot 2$ mm.). The undulating flickering motion of these cilia can with a little care be distinguished from the similar flame-like movements of the cilia within the duct of the glandular sac. Both are obvious when the animal is slightly compressed under a cover-slip and viewed from the dorsal side. The two movements are very close together, but the nephrostomial flame does not follow round the acute angles of the pigmented duct as the flame inside the duct naturally must, but takes a straighter course. Other small flickerings are seen in this same neighbourhood, produced by cilia on the walls of the pre-collar cavity main chamber: one of these beats just externally to, and parallel to, the base of the branchial vessel (text-fig. 2). As there are no other such cilia in any other somite, these may have some relationship to the nephrostome.

TEXT-FIG. 27.



Excretory cells in ventral body-wall: surface view, as seen in life after treatment with methylene-blue.

The several parts of this organ can be homologised with the corresponding parts of the various types of nephridium found in other Polychætes. The dorsal median aperture remains entirely anomalous, but the rest of the organ is really not so atypical as at first appears.

In several types of nephridium, *e. g.*, some Nereids (Goodrich, 1900), there are found tufts of cilia arising on and around the nephrostome (whether closed or open), beating into the coelom: structures with comparable appearance and function are described by Meisenheimer (1909) in other phyla. Beginning with a nephridium of such a form as this, the *Filograna* type may be deduced by imagining, firstly, the loss of the pre-septal portion of the funnel: secondly, the depression of the part of the septum to which the nephrostome is attached, into first a pit and then a finger-shaper diverticulum: and, lastly, the transference of the coelomic cilia from the margin of the nephrostome to a position just within the tube itself. There results, then, with no very fundamental change, a structure identical with that found in *Filograna*.

There are other cases described by Goodrich (1900) in the Syllids, and in *Polygordius*, in which very long cilia arise within the nephrostome-aperture, but it is stated that in these the cilia arise on the lip of the funnel and beat down its lumen; this, however, is the reverse of what obtains in *Filograna*.

The ciliated duct is lodged, in its proximal part, in the transverse ridge which crosses the collar-somite dorsally, and it is parallel to, and anterior to, the transverse muscle-band (*M.e.ch.tr.*). It crosses the dorsal longitudinal muscle-fibres externally to them, and the next part crosses the blood-ring, likewise externally to it (text-fig. 14).

The nature of the green granules has not been determined; they are resistant to reagents, and stain densely with hæmatoxylin stains or osmic acid. With a hope of determining their nature, some chemical tests for uric acid were performed on the living animal. These gave negative results as far as the glandular sacs were concerned, but as they gave evidence of the presence of excretory substances in other parts of the body they may be described here.

The tests used were, firstly, the murexide reaction, and, secondly, a modification of the Benedict method for detecting small quantities of uric acid. In the first case the method used was that described by Howland (1924), namely, the addition of strong nitric acid (with or without previous treatment with 50 per cent. alcohol), followed by evaporation to complete dryness. This last step is not so drastic here as in the case of Howland's *Paramœcia*, as the form of the animal is still distinguishable on the slide even after drying. Dilute ammonia was then added, but there was no positive reaction in any part of the body.

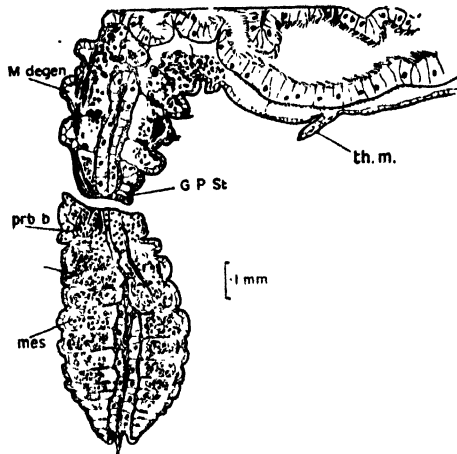
Hence the more delicate Folin-Trimble method was adopted. Weaker solutions than those given by Folin-Trimble (1924) were used, and the treatment was as follows. Some animals were placed in a measured volume of a solution of 5 per cent. cyanide, containing 2 c.c. of concentrated ammonia per litre. A quarter of this volume of arsenic phosphoric tungstic acid was added and the tube placed in boiling water for three minutes. Then it was removed and cooled in a beaker of water, after which the animals were examined under a $\frac{3}{8}$ -in. objective. There was no reaction from the glandular sac, but the granular cells lying in the epithelium in the region of the anus were coloured blue. On examining with a high magnification ($\frac{1}{2}$ -in. obj.) each globule in the cell was seen to be tinted blue. This reaction indicates that these cells are excretory in nature. The negative reaction of the glandular sacs may be due to the insufficient penetration of the fluids into the interior of the animal, or that, assuming that they are excretory, to the fact that the excretion is in the form of some substance other than uric acid. The deposition of and gradual accumulation of pigment in both these glands (as mentioned above, p. 128) favours the view that they are excretory in function. In a recently budded individual the sacs at their first appearance are colourless, and they become pigmented gradually. Further, in a stock which has lost its hind end in a bud and is regenerating another the anal gland is absent at first, but grows in size and increases in opacity as the

tissues become older. On the other hand, the bud which carries away the original hind end of the stock and which has passed through a period of particularly great activity has an abnormally large anal patch.

HISTOLOGY OF THE BUDDING*.

The internal and histological changes which accompany the development of the external form of the bud have been partially described by Malaquin in a series of papers dating from 1895 to 1925; the last of these (1925, 2) unfor-

TEXT-FIG. 28.



Horizontal section of hind end of a stock with a bud, showing disintegration of the stock as well as in the bud. The posterior end of the stock has commenced to regenerate new segments while the bud is still attached.

G.P.St., growing-point of stock; *mes.*, mesodermal masses in coelom; *M degen.*, degenerating muscles in stock; *prb.b.*, proboscis of bud; *th.m.*, hind end of thoracic membrane.

tunately escaped the notice of the author until the particular point with which it deals (namely, the origin of the blastogenic cells) had been already worked out. The results obtained agree in the fundamental points with those of Malaquin, but differ in some details from them: further, they include observations of cytological features not mentioned by him. The following description, therefore, will overlap somewhat that given by Malaquin, but it is necessary to repeat these observations here, in order to make the later part of the subject intelligible.

As a result of the internal changes which take place, the new individual,

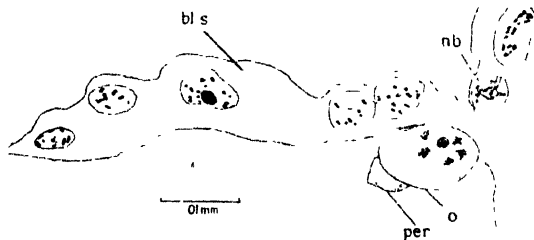
* In preparing the sections for this part of the work, a variety of histological techniques were tried: two, however, proved to be the most successful, and were almost entirely adhered to—these were Flemming-without-acetic followed by safranin and Bouin (with modifications) followed by Heidenhain's iron hæmatoxylin. The modifications of Bouin's fluid which gave the best cytological preparations were, firstly, Ezra Allen's chromic-urea-Bouin, secondly Duboscq-Brasil, and thirdly aqueous Bouin.

when quite complete, is to be regarded not merely as a fragment of the stock, which has been cut off and has regenerated a new head, but rather as a new young individual, inasmuch as its tissues are all young and newly differentiated.

As mentioned before (p. 122), the head, collar, and next succeeding somite are formed by the growth of a lobe of new tissue, and the other somites by the transformation of the posterior segments of the stock.

There are two points of interest concerning this anterior proliferation of new tissue. In the first place, since the alimentary canal is continuous throughout the stock and bud, until the time of freeing, the connection between the two individuals is such as might be described as a mouth-to-anus attachment. This is not strictly true, as the attachment is behind the mouth of the bud, but such a phrase emphasises the fact that, if there is this particular type of connection, then all the pre-oral somites (at least) must be proliferated anteriorly to the plane of fission. Another fact which is suggested by these observations is that the few anterior somites are atypical in form (*i. e.*, non-annular), and it is difficult to imagine how they could be formed by transformation of old abdominal segments. It is obvious, however, that neither of these remarks explains why

TEXT-FIG. 29.



Horizontal section through septal sinus of bud, showing neoblasts migrating and differentiating.

bl.s., blood-sinus; *nb*, neoblast-nucleus; *o*, oocyte; *per.*, peritoneal cell.

there is this special method of production of anterior somites, for the number of segments concerned in it is greater than is actually required to satisfy either of the two conditions.

The second point of interest concerns the manner in which the position of insertion of the new tissue and of the plane of fission are related to the septa and somites of the stock. The former is located immediately behind a septum and is therefore post-septal and the latter is inter-septal. Text-fig. 30 demonstrates this fact quite clearly. Behind the last septum of the stock (*s.n.*) there is firstly the newly-formed hind end of the anterior individual, then the bud-head and the two setigerous bud-segments, and, finally, the old and partially transformed segment with its mass of phagocytes; then the next septum (*s.n. + 1*). These two septa are originally adjacent: the newly-formed septa reach from the body-

wall to the new proboscis only ; hence the old ones, which stretch across the coelom and are attached to the old gut, are distinguishable.

The transformation of tissues which takes place in the posterior segments is of so complete a nature that, finally, there is not much more connection between the bud and its original segments than there is between an embryo and its parent, except the topographical position, for the tissues of these segments are entirely histolysed and replaced by embryonic undifferentiated cells. There seems to be considerable variation in the amount of time taken for the completion of this process. In some cases it progresses gradually, so that some part of each tissue retains its histological character, while the rest is in a condition of disintegration. In other cases there is a much more sudden and drastic change, during which the bud is represented by a structureless mass contained within the covering of epidermis.

This process of rejuvenation of tissues extends into the stock, but in this region the disintegration at any one time is only partial—in fact, there is probably never complete replacement here as there is in the bud. The histolysis in the stock is often confined to the abdomen, but sometimes extends into the thorax, and has been seen even in the brain. It happened many times during the course of this work that sections of individuals showing this phenomenon were discarded, as they were thought to have been injured during fixation. However, later, the condition was recognised in living animals and discovered to be normal : the histolysis of stock tissues is seen in text-figs. 5 K, 28, and in the microphotographs (Pl. 3). In the stock the degeneration is accompanied by the appearance of large orange-yellow fat-globules in the coelomic cavity and in the gut ; buds never contain such globules. It is not certain whether these are of the nature of food-reserves or are simply a useless product of degeneration ; but, judging from their presence in the gut-cavity and from the fact that they are probably discharged with the faeces, the latter interpretation seems to be indicated. In the bud, on the other hand, the material obtained by the disintegration of the tissues is utilised, at least partially, as food for the growing cells. Another comparable contrast between stock and bud is provided in the fact that, although in the latter the material contained in the phagocytes is all retained and utilised, in the stock there is not infrequently a rupture of the body-wall, through which some of the disintegrating masses are discharged.

The disintegration may be either intra- or extra-cellular. In the case of the gut the ciliated cells are discharged into the lumen, either singly or in groups, and, finally, are passed out at the anus. The other tissues are all attacked by phagocytes, though at the time of greatest activity large masses of muscle are seen to be breaking up independently ; but even these appear to be dealt with by the phagocytes later. The contents of the phagocytes are preserved by fixation in Bouin's fluid (whether aqueous or alcoholic), and stain after this very darkly with iron hæmatoxylin : they are blackened by fixation in fluids containing osmic acid. An endeavour was made to determine more accurately their nature by the application of methods of intra-vitam staining. On treat-

TEXT-FIG. 31.

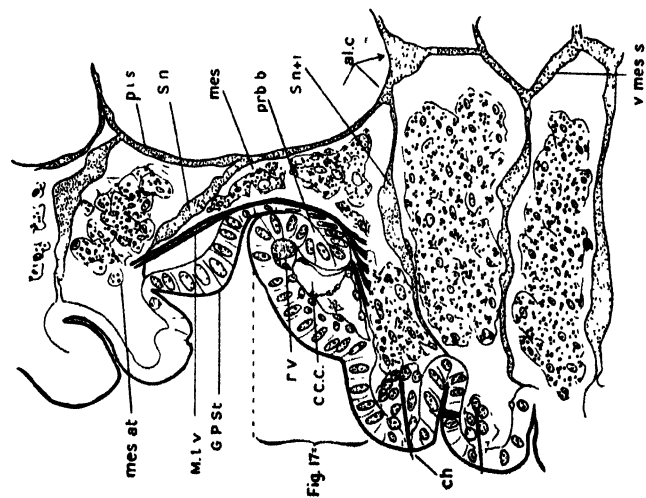


Fig. 30.—Horizontal section through junction between bud and stock.

Fig. 31.—Further enlargement of a portion of text-fig. 30 (Flemming-without-acetic preparation).

al.c., alimentary canal; *c.c.c.*, coelom of collar-somite of bud; *ch.*, chaetæ of bud; *G.P.St.*, growing-point of stock; *gr.*, nutritive granules in neoblasts in bud-head; *ec.n.*, nuclei of ectodermal cells; *mes.*, mesodermal masses in coelom; *mes.at.*, similar masses in coelom of stock; *M.L.v.*, ventral longitudinal muscle; *per.*, peritoneal cells; *p.i.s.*, peri-enteric sinus; *prb.b.*, proboscis or bud; *post-c.c.c.*, coelom of post-collateral somite of bud; *pre-c.c.c.*, coelom of pre-collateral somite of bud; *r.v.*, ring-vessel of bud; *S.n.*, most posterior septum of stock; *S.n.+1*, first old septum in bud.

ment with Sudan III. (Lorrain-Smith, 1907), the mesodermic masses in the bud assumed a bright orange-colour. Nile-blue sulphate was next tried (Lorrain-Smith, 1906), and it was found that this penetrated only very slightly into the interior of the animal and gave no results : to overcome this difficulty the body-wall was ruptured, and then it was seen that the globules in the cells which were extruded became greenish immediately—as these are originally orange in colour, this result is taken to indicate that the blue component of the stain was absorbed : hence it is concluded that fatty acid is present in the globules.

The phagocytes throughout most of the process remain extra-coelomic and lie in the cavity which separates epidermis and somatic peritoneum (normally occupied by the muscles only). A few, however, enter the coelom and are found lying against the masses of chloragogen-cells on the mesenteries, possibly discharging their contents into the chloragogen-cells. The presence of such large masses of phagocytes enlarges the extra-coelomic cavity and reduces the coelom to a space + -shaped in transverse section, in the centre of which is the gut. Text-fig. 5, B, shows a bud as it appears when focussed deeply below the surface: the reduction of the coelom is evident here. The opaque blocks which are described above (p. 122), and which are seen in this and all the other figures, are merely these masses of histolysing tissues. They persist in the bud after it has been freed (text-fig. 8), and there is evidence that at least some of their contents are used as nutriment by the actively growing cells, for the characteristic globules are found among embryonic cells in places in which they cannot have arisen originally. For instance, they are found in the bud-head, and there never has been any phagocytosis in this region, as it is an outgrowth of new tissue. The cells forming it (undifferentiated cells) wander in from the segment behind, and some at least of them arrive laden with the globules. Text-fig. 31 shows the head of a bud fixed in Flemming-without-acetic, and the blackened globules are conspicuous in this among the differentiating tissues. It is only in such new tissue that it is possible to demonstrate the utilisation of this nutritive matter, but such evidence seems to justify the assumption that the gradual disappearance of it in the freed bud is due to absorption of this kind, rather than to excretion.

Malaquin mentions the phagocytosis of the tissues and their replacement by undifferentiated cells. He comes to the conclusion that the cells in question are derived by proliferation of the gametocytes. He has found the two primordial germ-cells in the larva, and states that the cells derived by the repeated divisions of these “seront ensuite distribués dans les métamères, où ils deviennent les gonocytes extra-coelomiques . . . leur ensemble constitue une lignée germinale autonome dans l'individu, et continue d'une génération à l'autre” (1925, 1). Further, in his next paper (1925, 2) he states that “lorsque, tout au début de la reproduction asexuée, les gonocytes entrent en mitose active dans un ou plusieurs métamères, les cellules qui en proviennent prolifèrent au sein du tissu mésenchymateux nutritif, sous l'endothélium coelomique . . . Les éléments ainsi formés . . . sont les histoblastes (ou néoblastes)

migrateurs qui vont édifier les tissus nouveaux : nerveux, musculaire, épithélial, etc. . . .”

This double row of special cells is always found in the ventral body-wall. The cells are in close contact with the nerve-cords, lying practically superimposed, but rather mesially to them : they are against the basement-membrane of the epidermal cells, and hence are covered by the peritoneum : they extend from the anal papilla into the thorax. The present author does not agree with the cytological description given of them, and instead of saying that they are gametocytes, which on occasion produce tissue-cells, would prefer to summarise the facts by saying that these are the only cells in the body which retain the potentiality of active proliferation*.

When series of sections are examined, whatever the phase of the life-history, these cells are the only ones which are ever seen to be actively dividing. In the genital somites of sexual individuals a group of these cells situated just behind the posterior face of the anterior septum produces the sex-cells : these, sooner or later, pass through the peritoneum and come to lie in the coelom. In budding individuals these same cells divide actively and apparently produce both the phagocytes and the “Ersatzzellen,” or neoblasts. Also, they are responsible for the formation of the masses of chloragogen-cells on the mesenteries : these enlarge at times of great activity by the addition of cells from the ventral proliferating area. The same small cells are responsible for producing all of the new tissue at the terminal growing-point, details of which are given below. Malaquin describes the presence in the larva of two large mesoderm mother-cells distinct from the two primordial genital cells, but does not mention any further history, or divisions of these. In the full-grown budding animals that have been examined in the course of this piece of work the two cannot be distinguished : there are two groups of large cells with nuclei resembling those of the mesoderm mother-cells, but these are inactive and are themselves derived from the neoblasts.

The embryonic cells have already been referred to as neoblasts, and they are regarded as homologous with the cells of the same name in *Oligochaetes*. They have relatively the same position in the body and the same function. The apparent difference in their position in the *Oligochaetes* is probably due to the fact that with the approximation of the two nerve-cords the two intervening rows of neoblasts have been brought to a median position. The presence of neoblasts in *Polychaetes* is denied by Hämmerling (1924) in the summary which he gives of the literature on this subject, but the homology is accepted by Malaquin.

Potts mentions, in his description of *Trypanosyllis* (1913), the presence in the cushion of proliferating tissue of leucocytes and of “small nuclei with small scattered chromatin granules (*mes.n.*)” He also describes cells whose nuclei are large and contain a large nucleolus, and he states that “I am inclined to

* There are some mitoses seen in the newly-formed or forming tissues, but these are not numerous.

think that these wandering cells undergo a nuclear change, and become the actively dividing cells of the mesoblast." Judging by his figures, the previously mentioned cells with scattered chromatin-granules resemble more in appearance the neoblasts of *Filograna*, but there may be no histological similarity between the two.

The neoblasts are very strikingly different from all other cells, and hence are easily recognised. The nuclei are large in comparison with the size of the cell, the cytoplasm being reduced to a mere envelope. There is no nucleolus, and the chromatin is distributed round the periphery in small dense ovoid blocks (Pl. 7, fig. 2). These blocks are constant in number, and are heteromorphic. Further, they are always in the resting nucleus arranged in pairs, and the number of pairs agrees with that of the haploid number of chromosomes as counted in spermatocyte divisions, namely 13. Hence it is concluded that these blocks represent the condensed chromosomes. Malaquin describes these cells as having "nucléoplasme clair sur lequel se détachent 14-16 petites masses chromosomiques." No evidence is given for calling them chromosomal, and in his figures he does not demonstrate the regular ovoid shape which in reality distinguishes them so conspicuously from the chromatin masses in other nuclei: neither does he show them as existing in pairs.

When the neoblasts divide their nuclei pass through a complicated prophase which is reminiscent of heterotypic gametocyte divisions. A series of figures is seen before the appearance of the spindle, in some of which there is a very intimate association between the members of homologous pairs. The stages seen in sections have been interpreted in the following order.

The condensed chromosomes of the resting phase elongate, but do not form a continuous spireme. They may unite together in groups, as there are generally about six threads visible (Pl. 7, fig. 3). They pass later into a dense contraction figure, the various stages of which are shown in Pl. 7, fig. 5. At the beginning of contraction it is possible to see that a nucleolus is present, possessing the same staining properties as the chromosomes themselves. Also it is seen that the chromatin-threads are more or less U-shaped, and orientated with their free ends towards one pole of the cell. The chromatin-threads have a moniliform appearance during this phase, and sometimes there is an indication that the threads are double (Pl. 7, figs. 5 & 6): hence it is concluded that the homologous chromosomes are lying parallel to each other, and that the association between them is so close that it is difficult to distinguish the members of a pair. This phase, then, is exactly equivalent to a combination of the processes of synapsis and synesis as they occur in gametocyte divisions.

While in this condition of contraction the chromosomes condense again to a granular form, and on emerging enter another phase of distribution: they are still arranged in pairs, and the appearance now resembles that of diakinesis. The metaphase and final division of the cell now follow, during the whole of which the chromosomes are condensed in form. Pl. 7, fig. 8 shows the chromosomes collecting on to the spindle.

At some point during this division a stage is interpolated in which the chromosomes are connected together by slender filaments (probably linin threads) in a linear series (Pl. 7. fig. 7). A thick moniliform figure results, curved to adapt itself to the space inside the nuclear membrane. Often a horse-shoe curve is seen, but S-shapes and other irregular curves are also found. Thirteen blocks are countable on this series: sometimes they are distinctly double, but usually no line of division can be found in them. When they appear single, it is assumed that each block represents a pair of chromosomes so closely approximated that, at least in the stained preparations, there is no visible demarcation between them. This phase illustrates the heteromorphism of the chromosomes particularly well.

The preceding description applies to the neoblasts whether they are in the region of activity connected with bud-formation or whether they are proliferating in the sexual somites and acting as oogonia, or spermatogonia.

In previous cytological literature there are descriptions of chromosomal figures which agree in one or more particulars with those observed in the neoblasts of *Filograna*. The precise degree of comparison is variable, but in no case is there found a nuclear cycle in non-gametocyte cells which corresponds in all stages with that just described.

The previous papers will be discussed in two groups for the sake of convenience, although these will overlap to some extent. Firstly, the literature dealing with the persistence of chromosomes in resting nuclei (*i. e.*, "prochromosomes") is reviewed; secondly, the records of association between homologous chromosomes (*i. e.*, pairing of chromosomes at times other than during reduction divisions) are compared with the present case. Only those particular papers which show close cytological resemblance to the neoblasts of *Filograna* are mentioned here: a fuller summary of all the work which has a theoretical bearing on both subjects is given by Wilson (1925).

Prochromosomes of more or less convincing appearance have been described in both somatic and germ cells: from these descriptions a series could be built showing at one end homogeneous clear or granular nuclei, and at the other nuclei in which the whole of the chromatin is condensed into the chromosomes—intermediately would be the types in which the chromatin is more or less concentrated into distinct blocks or at centres, and in which these are more or less constant in number. The diagrammatic black-and-white appearance of the neoblast nuclei in *Filograna* represents the final stage of this series.

The figures of Stout (1912) and of Tischler (1910) show the closest approach to the present case. Both authors describe prochromosomes in somatic and germ cells, equal in number to the diploid chromosome number (see below for Tischler's remarks on fusion between members of a pair). Rosenberg (1904 and 1909) finds chromatic bodies which he concludes to be prochromosomes, in resting nuclei of many plants. Sykes (1909) finds "fully formed chromosomes" in the resting somatic nuclei of many plants. Overton (1906 and 1909) states that prochromosomes are commonly found in the cells of the root-tip in plants.

The various cases that he gives show the variability in the degree of concentration, or dispersion, of the chromatin: in some of the nuclei the chromosomes seem to be more of the nature of centres of concentration for the chromatin at the beginning of prophase, in others they are more definite and discrete. The descriptions of these authors mainly refer to plant-cells; King (1902) gives a zoological example—in the egg of *Bufo lentiginosus*,—and though many kinds of cell are included in these cases, yet one gathers the general impression that prochromosomes are most commonly found in germ-cells, cells in the tissues of the sexual organs, and embryonic cells (*i. e.*, cells of young embryos and cells in the root-tip).

The only evidence of the persistence of chromosomes in animal cells is derived from nuclei which show indications that an "architectural basis" of the chromosomes persists through interkinesis, though the actual visible (or stainable) structure is changed in condition. Such evidence is obtained by comparing the position and arrangement of chromosomes at their first appearance in prophase with that at the end of telophase; or, alternatively, by tracing chromosomal areas (or vesicular chromosomes) throughout the resting-stages. Although these cases are theoretically similar, they are not discussed here, as they are not structurally identical.

Of the authors mentioned above, Tischler, Overton (1906), and Sykes state that the prochromosomes are seen arranged in pairs. Tischler further emphasises the fact that the two members of some of the pairs are so intimately united that no dividing-line can be seen between them. This explains why the number of prochromosomes counted sometimes is less than the diploid number; such nuclei are called by Tischler "pseudohaploid." There is little, if any, sign of this union in *Filograna* in the resting neoblasts, but, as described above, it occurs at one stage of the prophase (Pl. 7, fig. 7). Stevens (1910) describes a paired arrangement of the chromosomes in resting germ-cells in *Culex*, the pairing occurring in telophase and lasting until the next prophase. Metz (1914), also Hance (1917), mention the possibility that this might happen. Stomps (1911) also thinks that the chromosomes may exist in a paired, or parallel, condition during interkinesis, as when they first come into view at the beginning of prophase they lie side by side.

There are authors who oppose the view that the darkly staining chromatic bodies which are seen in resting nuclei represent individual chromosomes. The paper of Digby (1914) may be mentioned among these, as it summarises very completely the opponents' point of view up to that date. In spite of what is said in the text of Digby's paper, the figures nevertheless do suggest prochromosomes in a marked degree, and even show the existence of the darkly stained masses in pairs. No definite opposition to the prochromosome theory since 1914 can be found.

The association in pairs of chromosomes during various stages of division is known from a considerable number of authors. Sutton (1902) figured equatorial plates of spermatogonial divisions of *Brachystola magna*, in which it was not

only demonstrated that the chromosomal complex consisted of a double set of elements, but also that on the spindle they were arranged in pairs, the two of equal size lying closely adjacent to each other. Montgomery (1906) found that homologous chromosomes lay parallel to each other in the spireme. Later, Stevens (1908), working on *Diptera*, stated that pairing occurs in follicle-cells, spermatogonia, and some embryonic cells; the same author in 1910 produced more evidence of the same nature, and suggested that it might possibly be the case that pairing of homologous chromosomes occurred in each mitosis of the animal. Sykes (1908), working on *Funkia*, describes both the early prophase threads, and also those in telophase, as being double, both in reduction and in somatic divisions. Janssens et Willems (1908) describe a paired arrangement in the kinesis of somatic cells in *Alytes obstetricans*. Gates (1908) describes the origin of chromosomes in *Oenothera rubrinervis* by transverse fission of the spireme, and figures them as lying at first in pairs: he also suggests that the members of homologous pairs were adjacent on the spireme. Muller (1909) states that the chromosomes are paired in the anaphases and prophases of somatic divisions in the root-tip of *Yucca*. Stomps (1911) states that the chromosomes of the vegetative nuclei of *Spinacia oleracea* are paired on the equatorial plates, and his suggestion that they are also paired during interkinesis was mentioned above. Dehorne (1911) emphasises the constant association of chromosomes in pairs in somatic nuclei in *Salamandra maculosa*. Metz (1914) says that the pairs of chromosomes exhibit a close association at all times in *Diptera*, and in 1922 produced further evidence in support of this statement: he concludes that the paired association of homologous chromosomes in the diploid cells, somatic as well as germinal, is characteristic of *Diptera*. Hance (1917) states that the chromosomes appear in the early prophase of somatic divisions in *Culex pipiens* in pairs, and Whiting (1917) supports this, adding that the homologues are still approximated in metaphase in the case of the spermatogonial divisions. The pairing of prochromosomes, as described by Tischler, Overton, and Sykes, has been mentioned above.

The theoretical conclusions to be drawn from this evidence may be completely summarised in the words of Strasburger (1907): "Die in der Kernplatten der diploiden Kerne der Erbsenwurzel nachzuweisende Anordnung der Chromosomen zu Paaren ist nicht nur eine Stütze der Individualität der Chromosomen, sondern auch ihrer Verscheidenheit."

There is another feature of great interest connected with the paired arrangement of chromosomes. It was mentioned that in the neoblasts of *Filograna* there is a synopsis stage, in the course of which there is apparently complete fusion of the two members of a pair, and also that there is a well-marked syneesis. Both of these phases are usually connected with maturation divisions, but this is not a unique case of such a phase occurring in somatic cells. Stevens in 1908 described the paired chromosomes in the spermatogonial divisions of *Diptera* as being twisted together. Tischler (1910) states that even in resting nuclei the prochromosomes may be so closely approximated that the dividing-

line between the members of a pair cannot be seen. Metz (1914 and 1922), in a paper on the Diptera, gives the most emphatic statement on this subject, saying that " Each pair of chromosomes goes through what amounts to a synapsis in every cell generation " and that the figures of division-stages often resemble haploid nuclei. He also states that in early prophase the association between members of a pair may be so close that they resemble a single element.

In none of these previously mentioned cases is there any suggestion of synesis occurring, so in that one particular the neoblasts seem to be as yet unique.

The theoretical importance attached to the behaviour of the chromosomes in these unexpected ways is very great. The occurrence of synapsis entails the possibility of exchange of material (or of crossing over) in somatic cell divisions, but it is difficult to find the possible significance of this. The only obvious consequence is that repeated opportunities for crossing would affect the percentage of cross-overs in the germ-cells when these are finally produced.

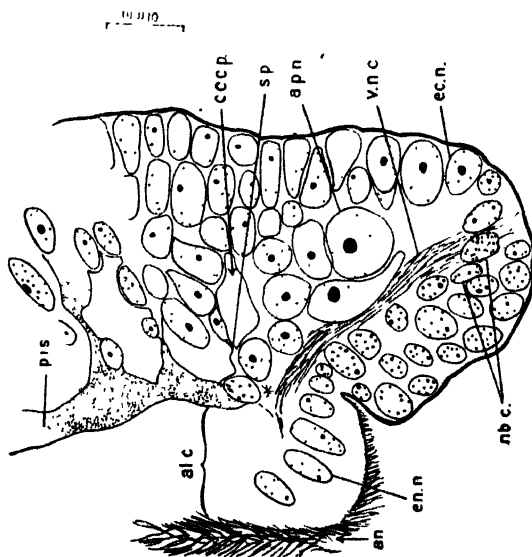
In conclusion, it is necessary to refer to two previous authors who figure a stage similar to that drawn in Pl. 7, fig. 7. Gates describes a comparable condensed linear arrangement, and Stout gives a second case, terming it a " discrete spireme " : the term is defined as indicating that the individual chromosomes are clearly distinct. In Stout's case there is a pre-synaptic univalent spireme and a post-synaptic diploid spireme, this second corresponding to the case of *Filograna*.

Differentiation of the cells produced by the proliferation of the neoblasts proceeds according to the ultimate fate of the cells produced. After division, the nuclei at first pass into the typical neoblast resting condition, and then, in the case of all except those cells which will remain as neoblasts, begin to differentiate. The first stages of differentiation, whether towards forming bud-tissues, phagocytes, chloragogen, or genital cells, are fundamentally similar, and the direction in which it ultimately proceeds seems to be determined by the position of the cell in the body or, in the case of regenerating tissues, by the position which the cell finally occupies after its settling. The cells produced by the neoblasts are capable of producing any kind of tissue, independently of whether it is regarded as theoretically ectoderm, mesoderm, or endoderm. The functional equivalence of neoblasts and germ-cells is further emphasised by the fact that sometimes an oocyte is seen in one of the bud-somites amongst the histolysing mass.

The presence of small nucleoli in nuclei which still show signs of the pairing of the chromosomes is taken as the first sign of differentiation of the neoblasts. Later the chromosomes lose their visible and discrete identity and the nucleolus enlarges. Text-figs. 32 & 33 show these stages of differentiation. Text-fig. 29 shows the nuclei among chloragogen-cells on a mesentery ; text-fig. shows a similar stage in the differentiation of neoblasts into endoderm. Text-fig. 32 shows the development of the coelomic sacs at the hind end of a bud.

The neoblasts are described by Malaquin as mesoblastic, but it is doubtful

TEXT-FIG. 32.



TEXT-FIG. 33.

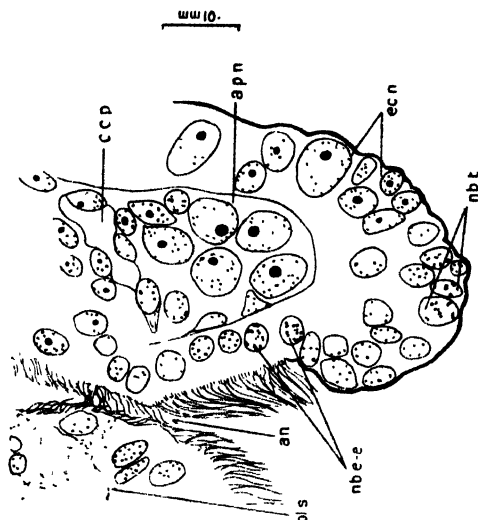


Fig. 32.—Horizontal section through anal papilla and posterior coelomic cavity of a bud, to show the terminal neoblasts.

Fig. 33.—The same as fig. 32, but showing particularly well neoblasts at junction between endo- and ecto-derm; terminal neoblasts also seen. Nuclei only are drawn in these two figures, cell-outlines being omitted. Both figures show early stages of differentiation of neoblasts into tissue-cells before the nucleolus appears.

alc., alimentary canal; *an.*, anus; *ap.n.*, nuclei of cells of anal papilla; *bl.s.*, blood-sinus; *c.c.p.*, most posterior coelomic cavity; *ec.n.*, nuclei of ectodermal cells; *en.n.*, nuclei of endodermal cells; *nb.c.* & *nb.t.*, terminal neoblasts; *nb.e.e.*, neoblasts at junction between ecto- and endo-derm; *pis.*, peri-enteric sinus; *sp.*, most posterior septum; *v.n.c.*, ventral nerve-cord.

whether they can be said to belong strictly to any one of the three primary cell-layers. Malaquin (1905) has traced them into the anal papillæ, but it is possible to trace them even among the most terminal cells of the outer posterior wall of the papilla. At the extreme hind end of the papilla is a gap in the thickness of the external cell-layer, and here are found a few neoblasts with the typical resting (or sometimes active) nuclei (text-figs. 32 & 33). The nerve-cords extend through the papilla to this terminal point, and the neoblasts are found, as in the abdomen, adjacent to, and dorsal to, these nerve-fibres. Also, between the last intestinal (ciliated) cell and the first ectodermal (non-ciliated) cell are inserted more of these undifferentiated neoblasts (text-fig. 33). Although these have not certainly been seen in division, it is probable that they are concerned in providing the cells required for the elongation of the ectoderm and of the endoderm. The particular situation on the series of neoblasts, where there is proliferation to produce the new coelomic sacs, is marked * in text-fig. 32: it is immediately anterior to the solid mass of cells in the papilla.

The whole of the histological processes involved in the formation of a bud show that there is, in this method of reproduction, an entire disregard of "cell-layers." Further, this description has made intelligible a previous remark concerning growing-points. It was said that when a bud is developing it does not in reality possess two growing-points. Descriptions of bud-formation generally convey the idea that the development of the anterior end of the bud is the result of the activation of a growing-point removed from the hind end; this is not strictly accurate. The increased activity is shown by all the posterior segments equally, and the formation of the head is not due to proliferation of segments quite in the ordinary sense. Cells accumulate here, but there are comparatively few cell-divisions taking place: those that are seen are scattered throughout the tissues, and the cells dividing are by this time more or less differentiated. On the other hand, individuals which begin to regenerate the hind end while the bud is still attached do have a second growing-point, but this is terminal in regard to the future individual, and hence in no way abnormal. It would be interesting to know whether, in cases which are able to regenerate a very large number of anterior segments, the neoblasts of the original segments are capable of producing them all, or whether in such a case there is more active cell-division in the newly formed tissues. For example, Allen (1923) describes an individual *Procerastea* in which 31 segments were regenerated anteriorly from an original piece of three segments.

It is interesting to compare the results of Hyman (1916) and Hyman and Galligher (1921) on axial gradients in budding *Oligochætes*, with the course of events in *Filograna*. According to Hyman, the first sign of the production of a bud in *Æolosoma* is the appearance of a zone of high metabolic activity in the neighbourhood of the region where the bud-head will arise. Later, this increase in activity spreads over all the bud-segments and becomes more strongly marked, so that at the time of freeing (or soon after), when de-differentiation of tissues and re-organisation are taking place, the gradient all along the bud is

considerably higher than at any point in the stock. In the Naids, however, there is no early increase in metabolic rate at the plane of fission, but later, when differentiation of tissues is taking place before and behind this level, the rise is detected: with the development of the bud-head the bud develops an independent gradient, similar to that of a non-budding individual. Hyman mentions that the gradient of *Autolytus* is quite like that of the Naids, but does not mention *Filograna*. It would be expected that as soon as embryonic tissue begins to accumulate in the region of the bud-head, there would be a rise in the gradient at that level. In the absence of experimental data, however, this question cannot be discussed.

SUMMARY.

1. Data are given which show that in *Filograna* there is much variation in many of the external features, including those which are supposed, according to some authors, to distinguish *Filograna* from *Salmacina*. Hence it is concluded that these two forms are not separate genera, but should be both included in the genus *Filograna*.

2. The course of the ciliary currents in the tube is as follows:—Water enters the posterior end of the tube: when it reaches the thorax it is all directed dorsally by the thoracic membrane and passes out of the tube by the dorsal portion of the anterior aperture. The branchial (feeding) current collects from a more ventral field. (Text-fig. 2.)

3. The longitudinal muscles are well developed. Their anterior subdivisions form the muscles of the collar and branchiae. Circular muscles are visible in the achæitous (*i. e.*, post-thoracic) zone only. It is suggested that these act as a compression-pump on the peri-enteric sinus and drive the blood in this forwards into the branchial filaments to expand these—or at least that they maintain the blood there under pressure. The gut-musculature consists of a sheath of circular fibres surrounding all the pre-abdominal region of the canal. In connection with the uncini there is an interesting musculature mechanism—a layer of turgid vacuolated cells in the parapodial wall is arranged to act as a passive spring-like opposition to the retractor muscles of the uncini. (Text-fig. 8.)

4. The central nervous system is of a primitive Annelid type. There are two ventral cords widely separate, in close contact with the epidermis. Each branchial filament is supplied with two nerves, one internal or mesial, and the other external or lateral: the latter bifurcates in each filament. (Text-fig. 5.)

5. The blood-spaces are of the nature of open sinuses, except anteriorly, where true tubular vessels are present. The main peri-enteric sinus surrounds the gut from the hind end of the proboscis to the anus, and is a continuous uninterrupted cavity. The blood in it spreads into the mesenteries and dissepiments, giving rise to dorsal, ventral, and inter-segmental channels: these

are open canals with no intrinsic epithelium. The blood in them spreads in an extremely thin film over the basement-membrane of the epidermal cells. Anteriorly there is an annular vessel round the proboscis, from which branchial and collar vessels arise. The walls of the vessels and sinuses are formed by the membranous peritoneum only. Movement of the blood is effected by anti-peristaltic contractions of the thoracic gut-muscles and by movements of the body: the circular muscles in the body-wall probably aid directly.

The form of the blood-system is considered to support the hypothesis that the cavity of the blood-system in Annelids represents (or has been derived from) the blastocoel of the embryo.

6. One pair only of excretory organs is present, lying in the collar-somite, and having the form of simple S-shaped tubes. The mesial ends of these unite to form a common terminal duct which passes dorsally through the prostomium, and opens terminally. Internally there is a granular enlargement on the tubes—the glandular sac: a pore places the cavity of the "sac" in communication with the coelom of the somite anterior to the collar, and hence is a nephrostome. A large flame ($200\ \mu$ in length) arises near the nephrostome and beats into the anterior coelom. The cilia in the excretory duct are also long and flame-like.

7. Buds are abundant during spring and early summer. Sexual individuals are mature (σ) and buds rarer during summer and autumn. A stock bearing a bud is generally asexual, and the bud itself is always asexual. The eggs develop in the calcareous tubes of the parent until the embryo is almost ready to settle. Embryos developed during early summer enter a sexual phase in the same season, those produced later reach their first reproductive phase (asexual) next spring. Individuals last more than one year, hence after a sexual phase there is a return to asexual reproduction in the next spring.

8. In the formation of a bud, the anterior region, including branchia, prostomium, collar-somite, and the next succeeding somite is formed by an outgrowth of new tissues at the plane of fission. The original stock-somites posterior to this are transformed into bud-somites, the anterior six or seven being transformed from abdominal into thoracic segments.

9. The interior of a bud is filled with opaque segmental blocks, composed of active phagocytes and embryonic cells. These persist for some time after the bud is freed, gradually diminishing in size and in density.

10. The stock regenerates the posterior end after the bud has been freed, and occasionally the regeneration begins while the bud is still attached.

11. The position of the plane of fission on the abdomen of the stock is not constant. There is a tendency for it to divide the abdomen, whatever the length of this, into two more or less equal halves. After a sexual phase (in which the abdomen is very long) the next bud produced is correspondingly long. At other times it frequently happens that the abdomen divides when it contains twice as many segments as the thorax. There are many variations of these types of configuration, and many irregular and exceptional cases.

12. Two abnormal buds are described in each of which a bud-head is being

produced terminally and posteriorly. It is further peculiar that in both the bud is attached to one half only of the stock.

13. The production of a bud entails a complete histological disintegration and regeneration of bud-tissues, and is accompanied by a similar but much less complete process of rejuvenation of stock-tissues. The cells concerned in the phagocytosis and replacement of tissues are derived from neoblasts in the ventral body-wall. The cells produced by these neoblasts give rise to ectodermal, endodermal, and mesodermal structures indifferently, and are probably identical with the cells which are responsible for the growth in length of all the tissues of the animal at posterior growing-point, independently of budding phenomena.

Neoblasts are identical with the sex-cells (*i. e.*, oögonia and spermatogonia).

Nuclei of neoblasts in the resting-stages possess definite chromosomes (pro-chromosomes) arranged in pairs in an otherwise perfectly clear vesicle.

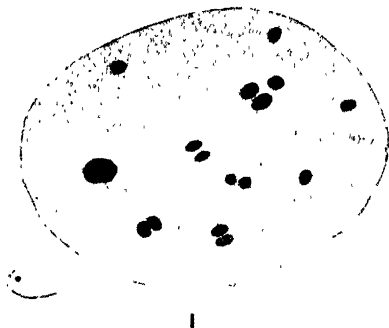
In every division the neoblasts pass through a contraction phase which strongly resembles the "synsinesis" phase seen in gametogenesis, and is either preceded by or followed by a synaptic union, during which the individuals of a pair are so intimately associated that no line of division can be seen between them.

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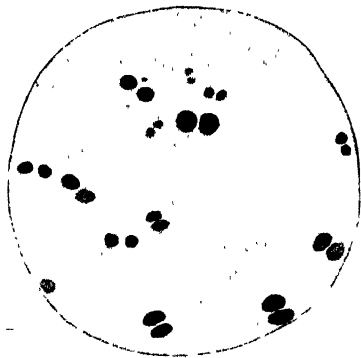
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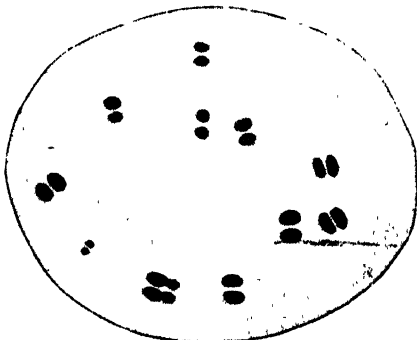
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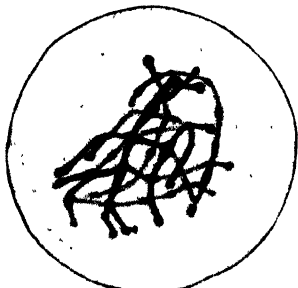
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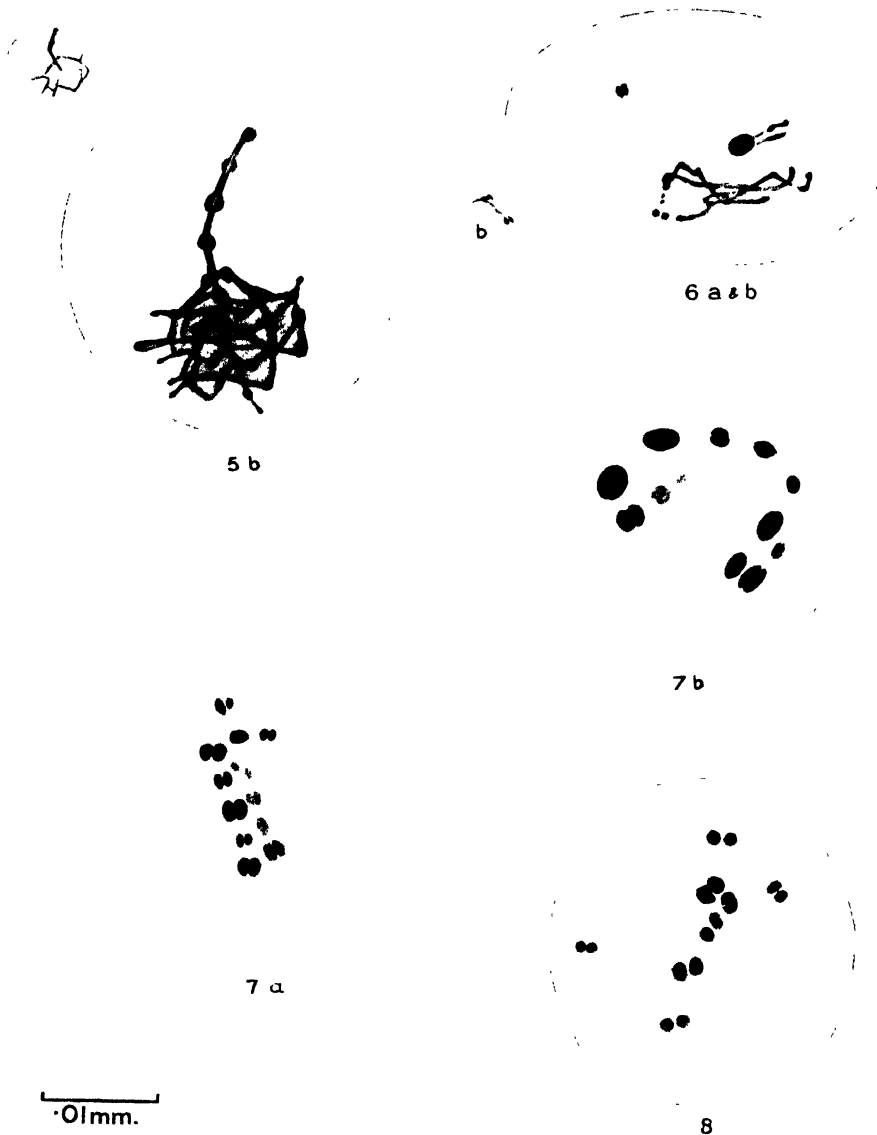
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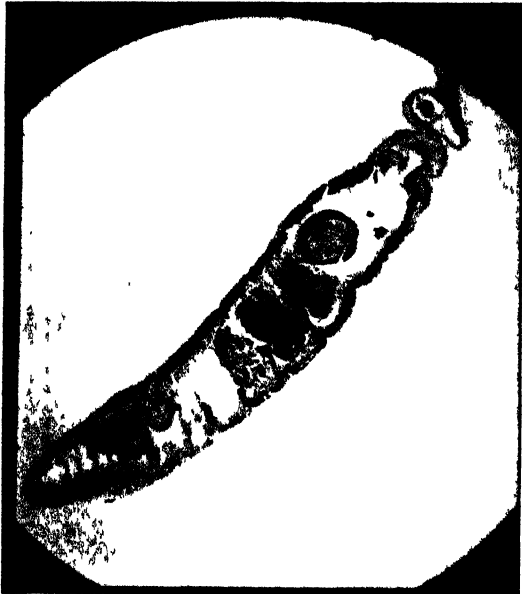
FILOGRANA

NEOBLAST



IMPLEXA.

NUCLEI.



FILOGRANA

BUD



1



2

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FORMATION.

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EXPLANATION OF THE PLATES.

PLATE 7.

Drawings of neoblast nuclei in resting and in division stages.

The small outline drawings represent camera-lucida tracings made under an oil immersion lens, the scale being indicated. The enlargements were made without aid from the camera lucida.

- Fig. 1. Neoblast nucleus at an early stage of differentiating into an endodermal nucleus: a nucleolus is present, and the chromosomes are losing their paired arrangement.
- 2-8. Stages of division of neoblast nuclei.
- 2 a & b. Resting neoblast nuclei, showing the condensed form and paired arrangement of the pro-chromosomes.
3. Spireme stage.
4. Beginning of contraction, or "synesesis" phase.
- 5 a & b. Slightly later stage, showing "synesesis" complete.
- 6 a. Portion of a nucleus at the stage of transition from "synesesis" to "diakinesis."
- 6 b. Portion of a thread from the other half of the same nucleus, showing its double nature.
- 7 a & b. Stages of "discrete spireme" in which the chromosomes, in pairs and more or less fused, are arranged in a linear series.
8. Early metaphase.

PLATE 8.

Micro-photographs. (In all cases fixation was with Allen's Bouin and staining with iron hæmatoxylin.)

- Fig. 1. Longitudinal section of individual showing first signs of budding: the thickened patch of epidermis is the beginning of the bud-head, and the collection of phagocytes is seen internally. The stock has sexual organs in this case—three segments testis, and a few small ova posterior to this. (Photographed under a $\frac{2}{3}$ -in objective.)
2. Horizontal section of hind end of stock with bud, showing an extreme case of degeneration of bud-tissues. ($\frac{2}{3}$ -in. objective.)
 3. Oblique section of hind end of stock and bud-head, showing disintegration of the stock tissues (alimentary canal and muscular tissues). ($\frac{1}{3}$ -in. objective.)
 4. Horizontal section of hind end of stock, showing histolysis of tissues; also, the presence of large ova-like cells in the coelom. The new posterior growing-point of the stock is seen on the right behind the last parapodium.
 5. Horizontal section of a bud after freeing, showing histolysis and regeneration of tissues (alimentary canal and muscles) still proceeding. ($\frac{1}{4}$ -in. objective.)

A Ceratioid Fish (*Caulophryne polynema*, sp. n.), female with male, from off Madeira. By C. TATE REGAN, D.Sc., F.R.S., F.L.S.

(With 3 Text-figures.)

[Read 20th March, 1930.]

THE fish described below was caught on 1st February, 1929: it was taken on a long line, in deep water, off Funchal Bay, Madeira, by a fisherman fishing for Espada (*Aphanopus carbo*). It was preserved, and in September last year was seen at Madeira by Dr. G. S. Carter, of Glasgow University, who made a sketch of it, which he sent to me, and who offered, if the fish were of interest, to ask to have it submitted to me for examination. At my request he wrote, and the fish has now been received from Mr. R. England, British Vice-Consul in Madeira, who sent it in charge of his son Clifford, and has presented it to the British Museum (Natural History). I have to acknowledge, with thanks, the assistance I have received in describing this fish from Miss Ethelwynn Trewasas, B.Sc., whose notes and sketches have been most valuable, and who has prepared sections to show the lateral line structure.

The fish, which measures 210 (145 + 65) mm in total length, belongs to the order Pediculati, the members of which are distinguished by having the first ray of the dorsal fin, termed the illicium, placed on top of the head, and modified into a line and bait, and to the suborder Ceratioidea, which includes the oceanic Angler-fishes: these are generally blackish, have a luminous lure, and are remarkable for having the males dwarfed and parasitic on the females.

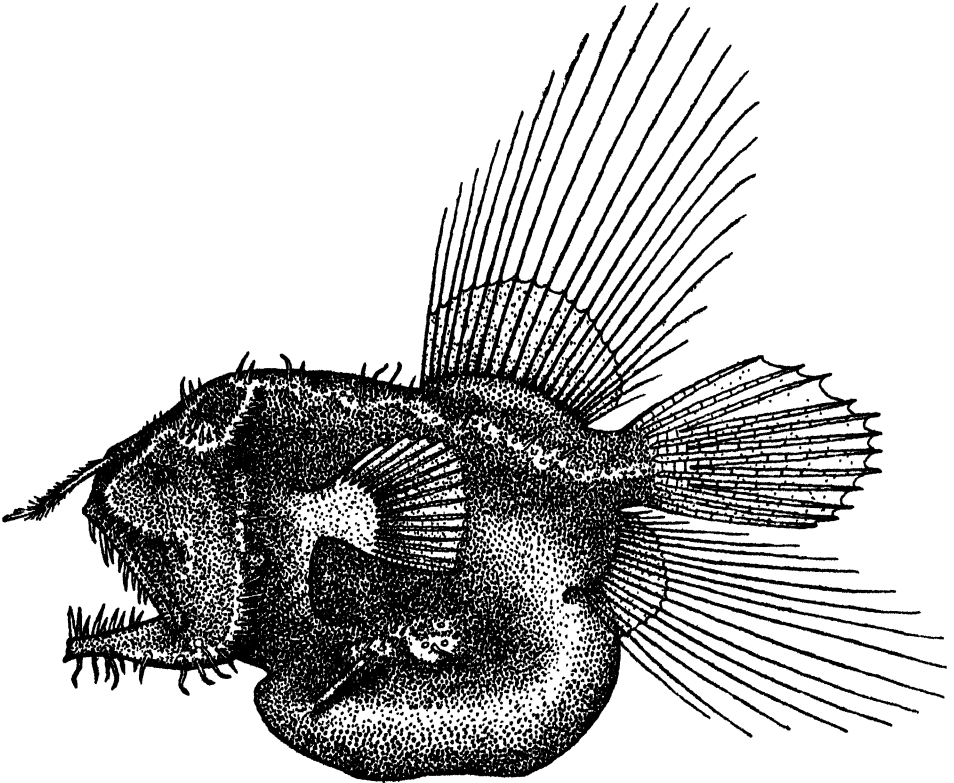
The fish represents a new species of *Caulophryne* (*C. polynema*, sp. n.), distinguished from *C. jordani* Goode and Bean, the other known species of the genus, by the filaments on the stem of the illicium and by the more numerous rays of the dorsal and anal fins (D. 22, A. 19, in *C. polynema*; D. 15-16, A. 14, in *C. jordani*).

The abdomen is greatly distended by a fish that has been swallowed, the head of which has been digested, although its caudal fin can still be seen in the mouth of the *Caulophryne*. The fish swallowed is at least 230 mm. long; it has the form of a Stomioid or of a *Lampanyctus*, but cannot be determined without removal. It may be recalled that other examples are known of Ceratioids that have swallowed fishes larger than themselves, but

the only one that parallels *Caulophryne polynema* is the type of *Melanocetus johnsoni* Günther, which took a bait and was caught, also on a long line off Madeira, although its stomach was distended by a *Lampanyctus* more than twice its own length.

Allowing for the displacement forward of the lower jaw, and backward of the anal fin, by the swollen abdomen, *Caulophryne polynema* seems to be very similar to *C. jordani*, except for the differences already noted. But some remarks on the fins, illicium, lateral line, and dwarfed male may be of interest.

TEXT-FIG. 1.



Caulophryne polynema, female with male ($\times \frac{1}{2}$).

The pectoral fin has fifteen or sixteen rays; the caudal has eight well-developed rays, the middle four forked, and a small adnate ray above and below. The rays of the dorsal and anal fins are slender, elongate, tapering to fine filaments, and connected by membrane only towards the base; some are broken, and it is not certain that any are complete, so that the figure is to some extent a restoration; but it has been considered legitimate, for example, when two broken rays occur between two others about 100 mm.

long, to restore them to the same length. The last few rays are close together at the base, and are inserted alternately right and left.

The stem of the illicium is about 20 mm. in length; it is pigmented proximally, and the pigmented area extends along the anterior surface, tapering distally; at the junction of the pigmented and white areas there is on each side a series of long, slender, translucent filaments, many of which are branched; as the white area broadens distally numerous other filaments originate from it. The stem of the illicium ends somewhat abruptly, and at its end, but on the right side, two appendages are attached; these are stouter than the filaments, but are translucent, except at their somewhat expanded distal ends, where they contain a number of minute opaque bodies, probably luminous. It is probable that the end of the illicium has been bitten or broken off, and the terminal appendages may represent two filaments that have grown and altered in structure since the damage was done. It may be recalled that in *C. jordani* the illicium ends in a tassel of long filaments.

TEXT-FIG. 2



Caulophryne polynema. Illicium ($\times 3$).

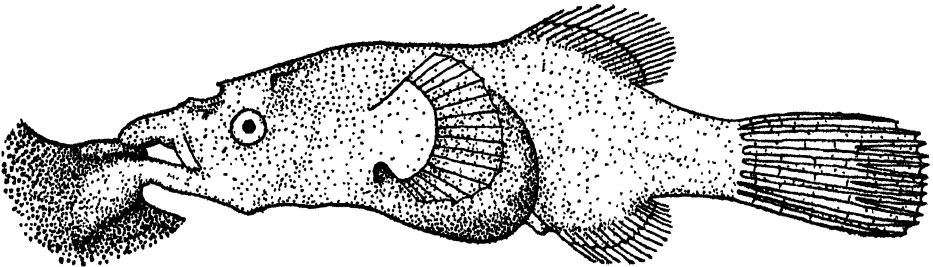
Formerly I have suggested that the filaments on the body of *Caulophryne jordani* might be elongate papillæ of the lateral line. In *C. polynema* there can be no doubt that the filaments on the head and body belong to the lateral line system, as they are inserted along nearly the normal course of the lateral line, the most notable exception being the presence of a few filaments on each side of the abdomen. The transverse commissures on the head are incomplete, and there are two series of filaments along each ramus of the lower jaw, a lateral and an inner or ventral. The skin near the bases of the filaments is lightly pigmented, and its yellow-brown colour contrasts with the black of the rest of the skin, marking the course of the lateral line very clearly. Many of the filaments are incomplete or missing, but when complete they are long, slender, tapering, and translucent, with an opaque thread within. At the base each filament arises from a rounded nearly white area, and when a filament is broken off a dot, which is the base of the opaque thread, is seen near the centre of this.

A section of a filament and of the skin near it shows that the filament consists of very loose connective tissue enclosed in an epithelial layer; the

opaque thread is a nerve, accompanied by two small blood-vessels. The nerve is connected with a lateral line sense-organ at the surface of the tip of the filament; the blood-vessels form a capillary plexus below the sense-organ. There is no trace of a lateral line canal or of sensory pits in the skin in the neighbourhood of the base of the filament, and the only lateral line organs are situated at the ends of the filaments; they present an analogy to the olfactory organs of certain Tetrodontidæ (Regan, P.Z.S. 1902) in which the sensory surface is not sunk in a pit, but is exposed at the end of a stalk.

The male is attached, head downwards, to the female on the left side of her abdomen. He measures 21 (16+5) mm. in length. The skin is lightly pigmented. There is no illicium, but there is a median antrose spine, probably a projection of the mesethmoid, in addition to the paired sphenotic spines. The abdomen is somewhat swollen, no doubt by the developing testis. The dorsal and anal fins are relatively much smaller than in the female, but may

TEXT-FIG. 3.

*Caulophryne polynema.* Male ($\times 5$).

not be different in this respect from the fins of a female of the same size; the rays appear to be fewer in number than in the female (D. 19, A. 16); this difference may not be sexual, but may be due to individual variation. The pectoral has seventeen rays. The mouth is toothless, and the attachment to the female is effected by means of outgrowths in front of the snout and of the lower jaw; these are separately connected with a prominence on the skin of the female, which is subdivided and asymmetrical, the lobe connected with the upper outgrowth being developed on one side, that connected with the lower on the other. The line of junction of the upper outgrowth is clearly marked, but the fusion with the female is complete.

In essential characters, small size, small fins, absence of illicium and of teeth, the male is similar to the Ceratioid males previously described. The attachment to the female is nearly as in *Cerantias* and *Photocorynus*, but in these the upper and lower outgrowths unite in front of the mouth, although a groove on each side divides them laterally. In a former paper I suggested that in this type of attachment the male must first nip a piece of the skin of

the female between the ends of the jaws, that the anterior ends of the lips then fuse with the papilla so formed, and that subsequently the outgrowths of the male move the mouth away from the female.

Males are now known in four of the ten Ceratioid families, namely, Photocorynidæ (*Photocorynus*), Caulophrynidæ (*Caulophryne*), Ceratiidæ (*Ceratius*), and Linophrynidæ (*Edriolychnus*). In the first three of these the attachment is by means of outgrowths in front of the snout and of the lower jaw. In *Edriolychnus*, however, the main attachment is inside the mouth, which is choked up except for a tiny opening at the corner, an arrangement that would seem to have its disadvantages. Further discoveries of males, and of their methods of attachment, may throw new light on the inter-relationships of the Ceratioids.

Further information about the Ceratioids may be found in the following :—Regan, " Dwarfed Males parasitic on the Females in Oceanic Angler-fishes," *Proc. Roy. Soc. B.* **97**, 1925, pp. 386-400, pl. xx; and Regan, Dana Expedition, Oceanographical Rep. No. 2, "Ceratioid Fishes," pp. 1-45, pls. i-xiii, Copenhagen, 1926. Also in the two sets of picture postcards, with leaflets, issued by the British Museum (Natural History) at 6d. a set, and entitled "Oceanic Angler-Fishes."

Notes on the Habits and Development of *Lepidosiren paradoxa*. By
G. S. CARTER, M.A., Ph.D., F.L.S., and L. C. BEADLE, B.A. (Com-
municated by Dr. G. P. BIDDER.)

(With 1 Text-figure.)

[Read 3rd January, 1929.]

THE habits of the American lung-fish, *Lepidosiren paradoxa*, have been described by several authors, and especially by Prof. Graham Kerr (Phil. Trans. R. S. London, B. excii, 299) and by Mr. R. J. Hunt (Proc. Zool. Soc. London, 1898, 41) *. The observations on which both these accounts were based were made in the Paraguayan Chaco, where the fish is common in the swamps which cover a large part of the country. During a recent visit to the same district, we were engaged in breeding the young of this fish, and several points in its natural history, which have not previously been recorded, came to our notice.

The burrow, which the fish makes when the swamps dry, has been accurately described by Mr. Hunt (*loc. cit.*). It passes vertically, or sometimes obliquely, downwards into the soil to a depth of two or three feet. The opening is covered with a biscuit- or bun-shaped cake of mud, and the burrow is blocked at intervals by partitions of mud, provided with openings by which air can diffuse into the burrow. In the examples which we saw there was only one of these, but, according to Mr. Hunt, there may be several at intervals down the burrow. The fish lies coiled in an oval expansion of the burrow at its bottom.

The soil below the soft mud at the bottom of the swamp is a pure clay which is very impervious to water. The burrow is made in the bed of the swamp as it dries, and, as the mud is only one, or at most two, feet thick, the burrow passes downwards into the clay. Probably the impervious nature of this clay is of great importance to the fish. The burrow is always damp (as Mr. Hunt remarks), and in the examples which we opened there was a considerable amount of water in it, enough almost to fill the expanded portion in which the fish lies. This water is probably essential to the life of the fish in keeping the skin damp. When a *Lepidosiren* is left in the air without a protective covering of water, the skin quickly dries and the fish lives only a few hours. It is unlikely that it would survive for long in the burrow, if it dried completely. It seemed to us a nice adjustment between the habits of the fish and its environment, that this layer of clay below the

* A bibliography of the subject is given in Prof. Graham Kerr's article on *Lepidosiren* in Kaibel's 'Normentafeln zur Entwicklungsgeschichte der Wirbeltiere.'

swamp should be essential for its survival during the periods, sometimes of many months, when the whole country is dry. The cocoon of hardened mucus, with which *Protopterus* surrounds itself in its burrow, is presumably an adaptation to the same end. In the burrow of *Lepidosiren* there is no such cocoon, the clay apparently providing sufficient protection. Whether a similar layer of clay occurs in other localities where *Lepidosiren* is found is not known. The habits of the fish in the valley of the Amazon are described by Goeldi (Trans. Zool. Soc. London, xiv, 1898, 413), but he did not investigate the structure of the burrow.

Except in the expanded part at its bottom, the burrow exactly fits the body of the fish, and it must be made by its forcing its way through the clay by muscular contraction. The clay can be kneaded by the hand, but it is stiff, and the resistance, which the fish meets in forcing its way through it, must be great. It is therefore a striking witness to the great muscular power of the fish that it is able to drive a burrow vertically downwards into this clay to a depth of 3 feet.

The Indians often dig up the fish from its burrow during the dry weather and use it for food. In doing so it is not necessary to dig to the bottom of the burrow. As the part in which the fish lies is approached, it can be heard moving at the bottom of the burrow and often making a peculiar grunt. Their method is then to push a stick into the remaining part of the burrow, until it comes into contact with the mouth of the fish. The stick is caught by the fish in its mouth and seized by the strong palatal teeth. It refuses to let the stick go and is drawn out of the burrow.

This habit would perhaps be hardly worth recording, if it were not that another air-breathing fish of these swamps, *Symbranchus marmoratus*, which is entirely unrelated to *Lepidosiren*, has developed precisely the same habit, and is caught by the Indians in the same way. The parallel adaptation of these two fishes in overcoming the dangers of the dry season is itself remarkable. Their burrows are in similar positions and can be distinguished by the Indians only with difficulty. That they should both have this habit of biting a stick pushed into their holes is even more remarkable.

The lung-fishes leave their burrows as soon as the ground above them is again flooded. The dry season is usually the winter, and the swamps are filled again by the first heavy rain of the summer. *Lepidosiren* breeds early in the summer after rain, and therefore as a rule shortly after leaving the burrow. But in many years the swamps do not dry and the *Lepidosiren* do not hibernate in the burrow. It therefore seems unlikely that a period of hibernation is essential before breeding can take place. The year in which we were in the Chaco (1926-7) was a dry one, and in September 1926 almost all the swamps in which the lung-fishes are found were dry. The swamps were again flooded at the beginning of October, and the first

Lepidosiren, taken in the swamp, were brought to us on October 18th. We first saw the nests on November 20th, after heavy rain on the 5th-7th. The eggs in these nests had only just begun to segment, and the nests had, therefore, only recently been completed.

The breeding-nest, which is entirely distinct from the dry-weather burrow, has been described by Prof. Graham Kerr, and we have little to add to his description. The eggs are laid at the end of an almost horizontal burrow in the mud at the bottom of the swamp. The nest is made of dead leaves and grass collected by the parent and taken into the burrow. Among these leaves the eggs are laid. The male, which guards the nest, is found coiled round the mass of leaves and eggs in an expansion at the end of the burrow, where the nest is made.

At the time at which we were observing the development of the lung-fish, we were also making observations on the physical characteristics of the environment of the swamps, among others observations on the amount of dissolved oxygen in the water. We found that there was hardly ever a measurable amount of oxygen in the water just above the mud at the bottom of the swamp during the summer months, when the climate is tropical. The nests of *Lepidosiren* are made at this time, and the water in them would therefore contain practically no oxygen, unless a supply is somehow secured by the parent fish. While the larvæ are within the egg-capsule and for some time after they hatch, their respiration is aquatic, and the method by which their need for oxygen is satisfied therefore needs explanation. It has been suggested by Mr. J. T. Cunningham ('Animal Life: Reptiles, Amphibians, and Fishes,' Methuen, 1911) that the long vascular filaments on the pelvic fins of the male during the breeding-season serve the purpose of keeping up the oxygen-content of the water of the nest, the parent aerating his blood by breathing at the surface. This, if true, would be a curious reversal of the normal function of the blood of bringing oxygen from the environment for the use of the body. In this case oxygen would be excreted by the blood *into* the surrounding water. We have no observations of our own on the source of oxygen in the nest, and the point needs further work.

It can, however, be said that the respiratory needs of the eggs and young larvæ are low. We kept the eggs and larvæ of several fishes in our hut in the Chaco, while we were preserving material of the young. We found that the nests could be divided into two categories. The eggs of those which were normally made on the surface of the water, or in other places where the water contained a considerable amount of oxygen, were extremely difficult to keep alive in cultures. On the other hand, the eggs of species whose nest is in the mud, such as *Lepidosiren paradoxa* and *Symbranchus marmoratus*, lived well. That the insufficiency of oxygen in the water of the vessels in which the eggs were placed was the true cause of the death of

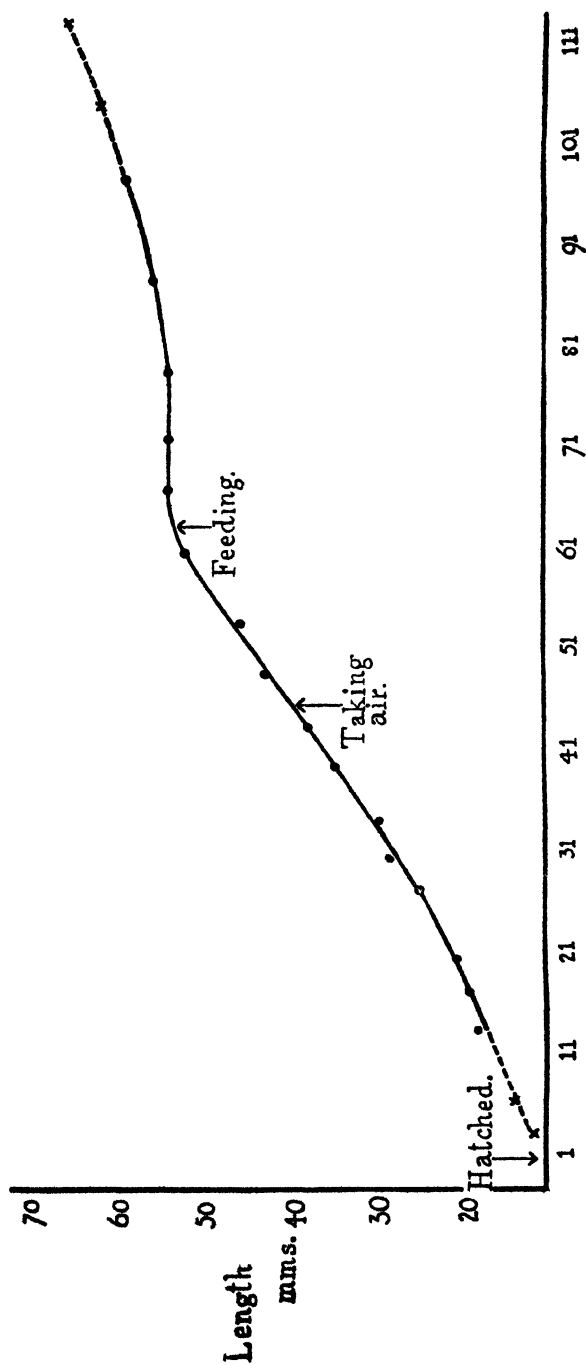
those of the first category, was shown by the fact that larvæ hatching from these eggs lived well, if they were able to get their oxygen from the surface, either from the air or from the surface-layer of the water. The larvæ of *Hoplosternum* (*Callichthys*) *litorale* and *Ancistrus anisitsi* both do this as soon as they hatch from the egg, and the ease with which they could be kept at these stages compared with those before the egg hatches was very striking.

These observations indicate that the eggs of *Lepidosiren* and *Symbranchus* are able to live in water in which the oxygen-content is comparatively low. Unfortunately, no direct estimations were made of the amount of oxygen in the water of the vessels in which the cultures were kept.

For the eggs of *Lepidosiren* and *Symbranchus* another difference between the conditions in the cultures and in their natural habitat was much more dangerous. The temperature of the mud at the bottom of the swamp is much lower at midday than that of the surface water or of the air. In growing these eggs, precautions had therefore to be taken to keep the vessels cool. This was done by making use of unglazed pottery bowls of Indian manufacture. In them evaporation kept the temperature of the water below 80° F., even when that of the air was as much as 110° F. The temperature so produced was about the same as that of the mud at the bottom of the swamp, and therefore of the nests. In these bowls the eggs were placed on muslin trays in a single layer, and they developed well, whereas in open dishes they died in one or two days. After hatching, the larvæ lose their sensitivity to temperature changes, and it was found unnecessary to use the pottery bowls. By these means we were able to watch the whole course of development in a single batch of eggs up to the time when the larvæ began to feed and were 2 inches long.

It has been previously noted (Graham Kerr, *loc. cit.*) that the egg is sometimes surrounded by a layer of jelly on the outside of the horny capsule, which is always present. This he has compared to the jelly-layer which surrounds the egg of the Amphibian. We found that this layer of jelly was always present in nests in which the eggs were at an early stage of segmentation, but that it disintegrated at the stage at which the descending lip of the blastopore had covered all but one-quarter of the surface of the egg. If this jelly is not needed at the later stages of the development of the egg within its capsule, it is difficult to see what function it can serve at these early stages. Our observations therefore support Prof. Graham Kerr's suggestion that it is a useless and vestigial character.

After the eggs hatch from the capsule, the two most noticeable crises in their development are the change in respiration at the time when the external gills degenerate (about 45 days after hatching at the temperature of our cultures), and the change from the absorption of yolk to the taking



Growth-curve of larva of *Lepidosiren paradoxa*.

of food by the mouth (about 60 days after hatching). Records of growth in length of the developing larvæ were kept, and a curve derived from these records is shown in the text-figure. The solid line of the curve refers to eggs from a single nest, and has been extended in each direction from records of other batches of eggs. In all, twelve batches were measured. The growth in the abnormal conditions of the cultures was probably slower than in the natural habitat, but there seems no reason to suppose that the effects of the conditions were more marked at one time than another. Without sacrificing a large number of larvæ, it did not seem possible to arrive at a better estimate of the growth than the increase in length. While the larvæ still contain yolk, the increase in mass is clearly no guide to the activity of growth.

Accepting, therefore, the results given in the curve as being very rough, it may still be deduced from the curve that the effects of the two physiological changes, mentioned above, on the growth of the larvæ are very different. The change in respiration had no appreciable effect on the rate of growth, whereas that in the method of feeding led, temporarily, to a very marked slowing in the rate. This presumably means that the blood was efficiently aerated by the gills or lungs throughout the period of the absorption of the gills, and the tissues were therefore unaffected by the change in respiration; but it shows clearly that not all important physiological changes in the development of an animal are reflected in changes of the growth-rate—an assumption which is sometimes made.

The larvæ were found to feed well on earthworms and on the liver of the large swamp-snail, *Ampullaria* (Graham Kerr, *loc. cit.*), but in the later stages they seemed to prefer the aquatic stems of the floating weed of the swamp (*Pistia*), eating not only algal growths around the stems, but also the stem itself. Probably this is the chief diet of the fish in its natural habitat. We could only find some small earthworm (*Aulophorus borelii*) in the mud of the part of the swamp where the *Lepidosiren* live, and these worms not commonly. The young fish of 2 or 3 inches in length would be unable to attack a live snail, although they would probably feed upon any dead one which they found by chance. There seemed little small animal life in this part of the swamp for them to feed upon except, perhaps, insects and their larvæ. It is interesting to note that Longman, in a recent article upon the habits of young *Ceratodus* (Mem. Queensland Mus. ix, 1928), records a precisely similar diet.

Until shortly before the time at which they begin to breathe, the young larvæ are colourless, with the exception of the yolk-sac, which is a creamy yellow, and of the bright red gills. At this time the black pigment-cells which are characteristic of the adult begin to appear in the skin, spreading from the tail and the dorsal side. The contraction of these cells at night has

been previously described (Graham Kerr, *loc. cit.*), but we have a few experiments upon them to record. We enclosed larvæ of about 2 inches in length for several days in a dark box and observed the behaviour of the pigment-cells. The box was very tightly closed, and there was little chance of sufficient light finding its way into it to affect the behaviour of the cells. We found that the pigment-cells were not, as might have been expected, continuously retracted in the dark. The larvæ varied considerably in their reactions to these conditions, but in some the normal rhythm of expansion at dawn and contraction at dusk was preserved for three days, the cells expanding and contracting at approximately the right time on each day. After this the rhythm became confused, and in other larvæ it was not preserved for so long a time. It seemed, however, that, in some larvæ at least, the rhythm had become impressed upon the animal and continued in the absence of the stimulus. That the stimulus was still effective was shown by the fact that larvæ, taken out of the box when the cells were contracted and placed in the light, immediately began to darken.

Reports of an Expedition to Paraguay and Brazil in 1926-7, supported by the Trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for the Universities of Scotland.

The Fauna of the Swamps of the Paraguayan Chaco in relation to its Environment.--I. Physico-Chemical Nature of the Environment. By G. S. CARTER, M.A., Ph.D., F.L.S., Lecturer in Zoology in the University of Glasgow, and L. C. BEADLE, B.A., Pembroke College, Cambridge, with Appendices by other authors. (Communicated by Dr. G. P. BIDDER.)

(PLATES 9-13, and 7 Text-figures.)

[Read 3rd January, 1929.]

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PHYSICAL AND CHEMICAL CONDITIONS OF LIFE IN A TROPICAL SWAMP.

I. INTRODUCTION.

The object of the series of papers, of which the present is the first, is to give an account of the bionomics of a tropical swamp. A complete account

of this subject implies descriptions both of the inorganic nature of the environment and of its effects upon the fauna, especially in the control of the type and abundance of the various members of the fauna, and in the production of adaptations of structure and behaviour by means of which they are able to maintain their life in the conditions of the environment. It is hoped to discuss all these aspects of the subject, but in the present paper only the nature of the environment will be considered. It is intended to complete the account with further papers on the fauna in relation to the environment.

The object is therefore to give as general an account of the bionomics of this environment as possible; but in carrying out the investigation we were particularly interested in one of the many problems of bionomics, namely, the relative importance to the fauna of the variations which occur in the different conditions of the environment, and the determination of the condition which, by its variations, is of greatest survival value to the fauna. This was so for many reasons, but especially because the tropical swamp is of peculiar interest to the zoologist from many points of view outside the field of bionomics—for instance, it has probably been of great importance in the evolution of the vertebrates—and it was thought that knowledge on this point would be of value in the study of these wider subjects.

The observations were confined to one type of tropical swamp in a comparatively restricted locality, a district in the Paraguayan Chaco. It is very probable that swamps in other parts of the tropics differ from these in many respects. The conclusions of a single investigation such as this cannot be extended to similar waters in other parts of the world except with great caution; but reasons will be given for thinking that conditions similar to those which were found to occur in these swamps are widespread in waters of this type in the tropics.

The conclusions to which the investigation lead have some bearings on the study of swamps in temperate countries. It is hardly surprising that a study of the conditions in similar waters exposed to the different climate of the tropics should throw some light upon the conditions in our own swamps. It will be found that the conclusion is reached that the most notable feature of the environment of the tropical swamp is the great lack of dissolved oxygen in its water, and that it is this characteristic which is of most importance to the life of the fauna. It seemed that this was largely caused by the complete stagnation of the water, and that one important factor in the production of this stagnation was the absence, in the warm nights of the tropics, of convection currents caused by the cooling of the surface. In the colder nights of temperate climates the layers of the water are mixed by these currents, and thus all parts receive sufficient oxygen for the use of the fauna during the next day. It appears that the fauna of the temperate swamp, which is often much more plentiful than that of similar tropical

waters, partly depends for its continued existence on the coldness of the nights and the convection currents thus set up, a result which does not seem to have been generally appreciated. It is clear that many other factors, and especially the photosynthesis of the aquatic flora, also play a large part in determining the amount of oxygen in the water. It is not intended to imply that the differences between the tropical and temperate swamp are wholly due to the difference in temperature.

The study of the bionomics of fresh waters has been actively carried on during the last twenty-five years, but it is nevertheless a comparatively new subject. It is therefore not surprising to find that much of the work has been rather preliminary to the study of the main questions at issue than concerned with those questions themselves. To the student of bionomics, work upon the chemistry and physics of fresh waters is clearly of this nature, and purely faunistic work is equally so. Further, he is forced to place in the same category the large amount of experimental work which has been given to the study of single conditions in the environment and the effects of variations in them upon animals, both in the laboratory and in the field. Knowledge of this kind is the basis upon which his work must be founded, and is therefore of essential value to him ; but wider investigations are needed for the solution of his problems. To gain a sound conception of the life of an animal in its environment, it is necessary to study the whole complex of conditions to which it is subjected, however incomplete that study may be ; to estimate the effects of changes in these conditions, not only singly but in combination ; and, finally, to compare the behaviour of the animal with that of other members of the same fauna. These problems are clearly extremely complex. They can only be investigated by research carried out upon the animal in its natural surroundings, and by simultaneous research into the nature of the environment and the behaviour of the fauna. But in view of the large amount of preliminary work which has been done, and of the success of some recent investigations of this kind—for instance, in the comparatively closely related environment of the sea,—it seems that the time is ripe for carrying the study of these problems some steps further in the fresh waters.

It is not meant to imply that the truly bionomic problems of fresh waters have been so far neglected. A great deal of work has already been done in this field, but it must be admitted that the results obtained are still very incomplete ; and, especially, that they are very unevenly distributed among the different types of fresh waters. The lakes and other large pieces of water have been accurately investigated. The work of Birge, Juday and others on the lakes of Wisconsin, and of many authors on various lakes in Europe, has resulted in a sound and extensive knowledge of this environment. Of very few other fresh waters is this true. To take one of the problems with which this paper is especially concerned, we know sufficient of hardly

any type of fresh water, except the lakes, to enable us to determine the condition of survival value in it. To classify the fresh waters on these lines would be entirely impossible at the present time. Yet the subject is an important one. Such a classification would be of as much interest from the bionomic point of view as one of any other kind.

The results of research upon the bionomics of temperate waters being so incomplete, it is not surprising to find that very much less has been done on tropical waters. A summary of recent work upon this subject has been given by Brehm (4). It is found to be almost entirely faunistic, with the exception of that of P. van Oye (9), on the conditions of life in the waters of the Congo and of certain rivers in Java, and that of Apstein (1) on the lakes of Ceylon. Accurate investigations of the chemical and physical conditions of the tropical freshwater environment are entirely lacking. The chief conclusions to be drawn from the work of these authors are: that the amount and type of the rainfall are the conditions of greatest importance to the life of the fauna; that they act by altering the chemical nature of the water by dilution and by bringing substances in solution from the land; and that other conditions, such as temperature and light, are of relatively little importance. Some of these types of water are closely related to the tropical swamp, but there appears to be no previous truly bionomic work upon the tropical swamps themselves.

It is to be noted, however, that it is precisely in the tropics that the most favourable opportunities for enquiry into the bionomics of fresh waters are to be found. Here the forces of Nature are at their strongest. Owing to higher temperature, growth is more rapid and decay more sudden. Evaporation is greater, and, by means of it and the tropical rainstorms, the chemical nature of the water is altered more greatly in a few hours than in as many days in a temperate country. These changes, and those produced in many other ways, being both greater and more rapid, will be easier to observe and will have more obvious effects upon the fauna and flora. Further, in these waters animals are living in conditions much closer to the limits of viability, and it is probable that, for this reason in addition, changes in the environment will have more marked effects upon them. Investigation of all bionomic problems should therefore be easier in the tropics. Probably only the inaccessibility of tropical waters has prevented workers in this field from investigating them more thoroughly.

When, in 1926, the opportunity of spending the greater part of a year in a tropical country occurred, it was decided to give a large proportion of the time to a study of the bionomics of the fresh waters of the district. The country to be visited was the Paraguayan Chaco on the latitude of the southern tropic. Here an almost perfectly flat plain stretches westwards from the Rio Paraguay towards the Andes, and much of the land within 100 or 150 miles of the river is covered with shallow swamps. It was

the conditions of life in these swamps which it was intended to study. For many reasons they seemed especially suitable ground for such an investigation. Although the country is so far south as to be on the southern boundary of the tropics, it has during the summer months an average mean temperature of $27^{\circ}3$ C. Both in this respect and in the nature of the rainfall, the climate during these months is distinctly tropical. The swamps are very shallow and in most years dry completely at the end of the hot season, which is here the period of greatest rainfall. Conditions in them should, therefore, show a large range of variation. They possess a very varied and interesting fauna, and are almost entirely unaffected by the spread of civilisation. Finally, owing to the hospitality of the South American Missionary Society and of its staff in the Chaco, it was possible for the authors to live at the stations of the Society. Thus they were able to attempt much more accurate work than otherwise would have been possible.

The plan of the research included as complete a survey of the bionomics of these waters as the circumstances allowed. It has been mentioned that it was intended to combine investigation of the inorganic environment with observations upon the fauna. The latter included enquiry into its behaviour, variation, and adaptation. The width of this plan must clearly result in less intensive research in each part of it; but it was thought that a problem such as that in view could only be approached by as broad an investigation as possible. In order further to broaden the plan, it was extended, after the work had been started, to cover certain other waters of the country, chiefly rain-water pools in the open pastures. It was thought that a comparison between the conditions in them and in the swamps, from which they differed greatly in some respects, such as the abundance of the fauna, might be of value.

In the part of the plan with which this paper is concerned, namely the investigation of the inorganic nature of the environment, the limitations imposed by the shortness of the time available and the difficulty of accurate work in an uncivilised country were great. For instance, it was thought advisable to undertake no chemical work more complicated than simple titration. In view of this restriction, and of the results of recent work on the sea as well as on fresh waters, the following chemical characteristics of the water were chosen for investigation :—

- (1) Temperature.
- (2) Hydrogen-ion-concentration.
- (3) Alkali-reserve (bicarbonate-content).
- (4) Carbon dioxide-content.
- (5) Oxygen-content.
- (6) Phosphate-content.
- (7) The penetration of ultra-violet light.
- (8) Salinity (in natural saline waters).

A few samples of water were brought home for inorganic chemical analysis, in order that the salt-content of the waters being investigated might be defined. The results of these analyses are given in the second appendix at the end of the paper. They are only sufficient to define the character of the waters studied, and it is not intended to draw biological conclusions from them. Further work was not done on the variations of these characters on account of the impossibility of carrying out such work in the field, and of the difficulty of bringing home samples of the size required for the analyses in good preservation and in sufficient number. Further, it seemed improbable that variations in these characters would be of importance to the objects of the research. The different inorganic salt-contents of waters of different types and from different localities are probably of great importance in determining the type of the fauna in each. But animals are chiefly sensitive to variations in the proportional amounts of the various substances present in the water, and the proportional changes are not likely to be great in the same water at different times of the year. The main subject of the investigation was the conditions of life in a single type of water and its seasonal variations, and these characteristics of the waters were therefore not studied further.

It is to be regretted that in the circumstances it was not possible to study the nitrate- or nitrite-contents of the waters, but it seemed that these determinations were not practicable in the field. Thus the phosphate estimations became of especial importance, since they were the only available approach to the ultimate food-sources of the fauna and flora.

It is clear that the discussion of the conditions of life in these waters requires some previous account of the country in which they are found and of its climate. This will be given in the first section of the paper.

The authors owe their opportunity of carrying out this work to grants made for the purpose by the Trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for the Universities of Scotland. They also wish to express their great debt of gratitude to the South American Missionary Society and to its staff, and especially to Mr. Andrew Pride, the superintendent of the stations in the Chaco, whose knowledge of the natural history of the district was of very great value to them. Their thanks are also due to Prof. J. Graham Kerr, F.R.S., and to Prof. J. Stanley Gardiner, F.R.S., for much help and encouragement throughout the work; and to Mr. J. T. Saunders, of Christ's College, Cambridge, and Mr. A. P. Orr, of the Millport Marine Biological Station, to whom they are also indebted for assistance and advice.

II. GENERAL DESCRIPTION OF THE PARAGUAYAN CHACO AND ITS SWAMPS.

El Gran Chaco is the name that was given by the Spaniards to the wide plains which form the western part of the basin of the Paraguay and Paraná rivers. These plains stretch from the hills which separate the basin from that of the Amazon in the north up to and beyond its southern limit on the latitude of Buenos Aires. Unlike the eastern part of the basin, from which they are separated by the main watercourse of the rivers, they are everywhere monotonously level, consisting of savannahs with occasional patches of woodland in some parts. In the south they form the pampas of the Argentine, and have long been enclosed; in the north, on the latitude of Paraguay, settlement has only begun in the last few years.

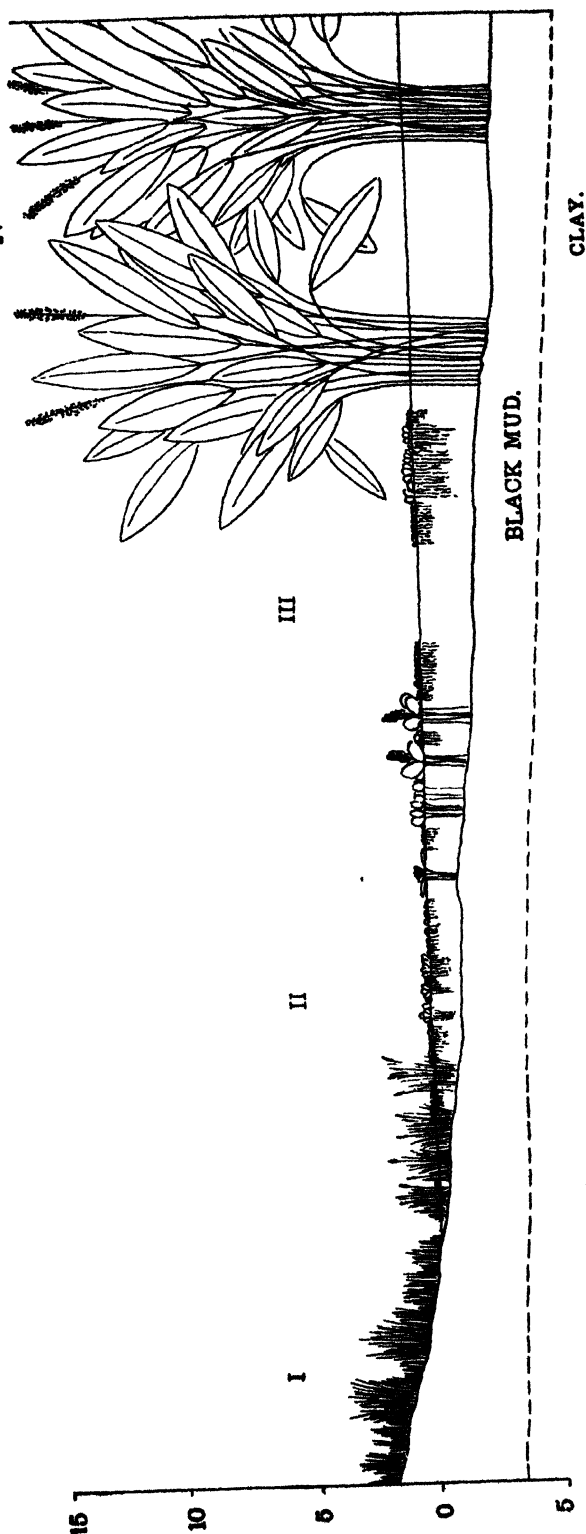
The part of this country in which the observations were made lies to the west of Concepción, in Paraguay ($23^{\circ} 30' \text{ S.}, 57^{\circ} 30' \text{ W.}$). Most of the work was done at the central station of the Mission, which is at a place called Makthlawaiya ($23^{\circ} 25' \text{ S.}, 58^{\circ} 19' \text{ W.}$), about 60 miles to the west of the river Paraguay.

In all this region the plain is so flat that no differences of level of more than a few feet occur over wide areas. The whole land has, however, a very slight slope towards the river. This slope is not more, and probably much less, than one foot to the mile, but is sufficient to give rise to a slow drainage over the country towards the east. In this way the local water is removed, but from the western part of the basin, which is much drier, very little water reaches the river. Although so small, the local differences of level are sufficient to give rise to very different types of vegetation. The rain is mainly in the form of heavy and sudden storms, and drains rapidly from the higher ground. Here there is found a dry woodland, mostly of thorny trees and shrubs, among which acacias and algarobas (*Prosopis* spp.) are very common. On the edge of these woods and occupying the ground of next highest level is an open grassland bearing the common palm of the country (*Copernicia cerifera*), often in such numbers as to form continuous groves. The palms stretch for a varying distance from the wood, but never reach the land of lowest level. Beyond them are open grassy plains, and in the centre of these the swamps. These different types of vegetation often occur within short distances of each other, but in other places each type may stretch over wide areas of country. It can hardly be doubted that their distribution is entirely determined by the slope and consequent drainage of the ground.

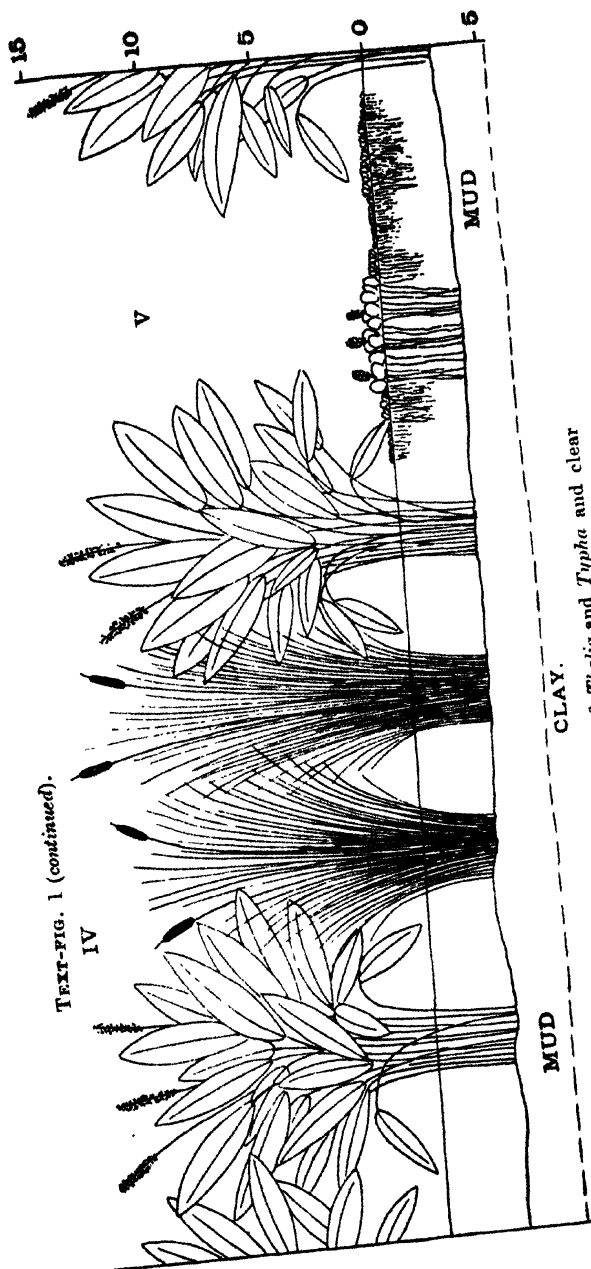
With the exception of the woodland, the whole country is liable to be more or less flooded. On the other hand, there is hardly any water which may not dry during a prolonged drought. Even during the drier months of a normal year it is usual for large areas of the swamps to dry.

TEXT-FIG. 1.

Diagrammatic cross-section of the swamp from its edge to the central region.



- I. Grassland at the edge of the swamp.
- II. Outer region of the swamp. Near the edge, shallow water with sedges and other plants. Beyond this, floating vegetation of *Pistia*, *Salvinia* and *Azolla* with various larger aquatic plants: *Nymphaea*, *Hydrocharis*, *Pontederia*, *Eichhornia*, etc.
- III. Open pool in this region.



TEXT-FIG. 1 (continued).

IV. Central region of the swamp, with large clumps of *Thalia* and *Typha* and clear water between them.

V. Pool in this region free from these large plants. Vegetation similar to that of the outer region of the swamp.

(Scale of height in feet.)

The low ground, which is occupied by the swamps, is in the form of very shallow valleys, generally running in an east and west direction. Thus the swamp is, as a rule, not more than a mile across from north to south, but may extend for many miles from east to west. The central part of it, which dries less frequently and for shorter periods, is filled with crowded clumps of tall Marantaceous plants (*Thalia* sp.) and of bulrushes (*Typha* sp.). These clumps grow to a height of fifteen feet above the water, and their leaves form a thick mass of overhanging vegetation, which casts a dense shade below it. Their stems rise from clear yellow water with no other vegetable life.

Towards the edge of the swamp, there is always a stretch of water in which these plants are absent. Here, and everywhere among the clumps of tall plants where small open spaces occur, the surface is covered with a blanket of floating vegetation in which *Pistia* and the water-ferns *Salvinia* and *Azolla* are predominant. Large areas of the water in this part of the swamp are choked with sedges, water-lilies, and other marsh plants. Stretches of water with no vegetation at the surface are rare. Apart from small pools in this outer part of the swamp, they are only to be found where land has been recently flooded and the vegetation has not yet had time to cover the surface.

The flatness of the land prevents the accumulation of the water to a greater depth than 3 or 4 feet. In some places the depth of the water in the swamp may be found to reach 5 or even 6 feet, but these are rare and are usually at places where the soil has been dug out. The bottom of the swamp is everywhere a black mud containing much gas. In it the foot sinks to a depth of about 12 inches. It is not more than 2 or 3 feet thick and passes downwards into a pure clay.

In text-fig. 1 a diagrammatic transverse section of the swamp is given. Photographs of different aspects of the vegetation of the swamps are reproduced on Pls. 9 and 10. figs. 1-6.

At a distance of about 100 miles from the Rio Paraguay the nature of the country alters suddenly. To the west of this limit, both the swamps and the palms are absent. The whole country consists of grassy plains alternating with large areas of dry woodland. There is no permanent water, but during a wet season the whole land may be flooded. At least for many miles to the west the plain is hardly less level than in the parts nearer the river.

During the last few years much of the country near the river, and in some places as far as the swamps extend to the west, has been enclosed to form large cattle-ranches. It is only altered by the destruction of the tall grass which formerly covered the open plain, and its replacement by a lower sward. Large areas are still unenclosed. Previous to this there was practically no cultivation.

Geology.—The geological structure of the country is simple. Throughout this part of the Chaco the subsoil consists of a fine-grained sand or silt, which reaches to within 12 feet or less of the surface, and extends downwards as far as borings have gone, and certainly for many hundreds of feet. It is everywhere waterlogged. The water obtained from it is very variable, being often undrinkably saline and as frequently inappreciably so. It is usual to find these differences in the water of two wells within a very few yards of each other and of the same depth. An analysis of a sample of drinkable water from such a well is given in Appendix II.

The silt is found over the whole country to the limit of settlement in the west, and probably far beyond it. In the western country, where the swamps do not occur, it passes upwards directly into a rather fine-grained and clayey soil, but in the eastern region there is between it and the soil a layer of 8 or 10 feet of pure clay. This clay occurs over the whole country in this region, and not merely in the beds of the swamps. It is very variable in colour, but is everywhere extremely impervious to water. The surface soil, except in the swamps, where it is the black mud mentioned above, is of the same nature as in the country to the west. It is yellowish when dry and entirely without stones.

The results of analyses of these soils are given in Appendix I.

It can hardly be doubted that the occurrence of the swamps only in the eastern part of the country is determined by the presence of this layer of clay. It extends over that part of the country in which they occur, and no further. In its absence the surface water must drain rapidly downwards into the silt, and, in a country in which the rains are occasional, this must prevent the accumulation of any permanent water. On the other hand, where this impervious layer is present, downward percolation of the water is prevented, and it collects on the lower ground to form the swamps.

Drainage.—Small streams flowing towards the Rio Paraguay are frequent. In the higher land they cut gulleys to a depth of 10 or 15 feet and are conspicuous, but, where they cross the lower land, they are often lost in the swamps which cover it. The surface water flows eastwards in these streams or drains towards the river by flowing over the land. The streams are very rapidly filled during a rainstorm, but in a few days the water drains from them and they begin to dry up. Frequently lines of pools, often very saline, are the only water which is left in the gulleys.

An analysis of the water of a very saline example of these pools is given in Appendix II. It will be seen that the density is 1·015, more than one-half that of sea-water. It is probable that this high concentration of salts is derived from the saline water of the underlying silt, to which the stream had cut its way. Everywhere else the layer of clay prevents the water of the silt from reaching the surface, and no evidence was obtained of its doing so.

The land in the eastern region, where the clay occurs, is lower than that to the west, which is drained by the silt, and an upward pressure of the water in the silt should therefore be present. The water rises in most wells sunk into the silt, giving evidence of the existence of this pressure. The pools are therefore filled continuously by this upwelling water of the silt, and became very saline by its evaporation.

Climate.—Meteorological data derived from records of the observations taken at the Central Station of the Mission at Makthlawaiya are given in the following table. The station is a recognized observation post of the Argentine Meteorological Service, and the observer and his instruments are under the supervision of the service. The authors have to thank the staff of the Mission for these data:—

Temperature.—

Average daily mean.	° C.	° F.
Summer (November–January)	27·3	81·1
Autumn (February–April)	23	73·5
Winter (May–July)	18·5	65·2
Spring (August–October)	23·5	74·4
Year	23·5	74·4
Yearly mean maximum	30·3	86·5
Yearly mean minimum	18·0	64·4

Average rainfall.—

	mm.	in.
Summer six months (October–March) . .	800	31·5
Winter six months (April–September) .	600	23·7
Year	1400	55·2

The figures given in this table are averages over a period of nearly thirty years, but the climate is very variable, and it is unlikely that any one year will adhere at all strictly to them. It will be seen from the records given below that this was the case in the year of the investigation.

The commonest type of weather consists of cycles of a week's or a fortnight's duration. For the greater part of this cycle a hot and relatively dry wind blows from the north and the temperature increases continuously. This wind blows only during the day, rising an hour or two after sunrise and falling at sunset. The nights are usually calm at the ground-level, but the movements of the clouds show that the wind persists at a higher level throughout the twenty-four hours. After several days of this weather a bank of clouds appears on the southern horizon and rises gradually until it passes overhead, accompanied by a southerly gale and frequently bringing with it a storm with much lightning. During such a storm, which may last many hours, as much as 8 or 10 inches of rain may fall. The change of the wind to the south is always associated with a large fall of temperature.

After two or three days of cooler weather, the wind returns to the north and the cycle is recommenced.

Rain is rare while the northerly wind is blowing, but the atmosphere is by no means absolutely dry. The wind bears with it a succession of light cumulus clouds, which pass over to the south to return either in the form of rain or heavy cloud with the southerly gale. The absence of rain while the wind is in the north is probably due to the high temperature at this time.

In a normal year the rain may fall at intervals of a week or a fortnight at the completion of each cycle, but it by no means always does so. In many years, periods of one or two months without rain are frequent, and droughts of six or more months sometimes occur. The intervals between the rains are usually longer in the cooler months, but in this respect, as in others, the climate is very variable. The periodic type of the weather is indicated in the records of rainfall and temperature given on Pls. 11 and 12.

From this description of the climate it will be seen that it is distinctly tropical during the summer months. The bionomics of the waters may, therefore, be expected to be of the tropical type in which successive periods of evaporation and dilution are the variations of most importance to the fauna. It will be seen from the description to be given below that this proved to be so. It will be found, however, that variations due to conditions external to the water were of less importance to the survival of the fauna than the more constant factors in the environment.

III. METHODS.

A small room was set apart by the staff of the Mission for the biological work, and in it most of the analyses of the waters were made. It was at a distance of about half a mile from the chief observation points in the swamp. Samples of water were collected in closed bottles and carried to this laboratory, where they were immediately opened and analysed. Occasional control experiments, in which the chemicals were added to the samples at the edge of the swamp immediately after they had been collected, showed that they underwent no appreciable change in the short time necessary to bring them to the laboratory.

The glassware and almost all the chemicals for the analytical work were taken to S. America from this country, and were therefore of the quality in general use at home. All the chemicals needed for making up accurate solutions were taken out in sealed glass tubes in weighed quantities. This was necessary in the absence of any method of accurately weighing substances in the field.

It was not possible to obtain distilled water in sufficient quantities for general use. Some was taken to the station and used for such purposes as making up indicator solutions and standard hydrochloric acid, but in

other cases clean rain-water was used. This was collected in an iron tank from a corrugated iron roof. It was shown to contain no phosphates and alkali-reserve (bicarbonates) of a strength of '0001 N. (.8 parts per 10^6). Most of this alkali was probably derived from particles of calcareous dust dissolved by the rain during its fall. The value is normal for rain-water.

Temperature.—Thermometers were put out in the swamp attached to a stake, and read, whenever practicable, daily. They included maximum thermometers of the broken-column pattern, horizontal minimum thermometers, and the non-recording type. Owing to the loss of several thermometers early in the research by interference by cattle, it was not possible to make the temperature observations as complete as had been hoped.

Hydrogen-ion-concentration.—The Sörenson indicator method was used for this estimation. Sealed buffer-tubes made up at home were used as standards. They were kept in the shade, and showed no variation from freshly made buffers after they had been brought home at the close of the investigation. The indicators used were the series of sulphone-phthaleines from thymol-blue to brom-cresol-purple. Indicator solution was made up at home, but in certain cases in which the supply was not sufficient, fresh solution was made from the dry substance and standardized for strength against the old solution and the buffers.

Alkali-reserve (Bicarbonate-content).—This was estimated by titration with N/100 HCl, using methyl orange as an indicator. N/10 HCl was taken out, and was standardised in the field against oxalic acid, which was taken out in weighed quantities for the estimation of ultra-violet light, and caustic potash. The N/10 HCl was found to keep very well in the hot climate.

Carbon dioxide-content was calculated from the values of the hydrogen-ion-concentration and the alkali-reserve by means of the tables given by Saunders (13). The total carbon dioxide is therefore estimated, including that bound, half-bound, and free.

Oxygen-content.—This was estimated by the Winkler process. Weighed quantities of sodium thiosulphate, potassium iodide, and caustic potash were taken out, and concentrated hydrochloric acid was obtained in Paraguay. Samples of water were collected in bottles of a known capacity of about 130 c.c. Owing to the large variations of the amount of the gas in the water this volume was found to be sufficient. They were filled within a larger vessel of about 750 c.c. capacity by means of a syphon by the usual method. Occasionally the samples contained mud and other suspended matter, but control experiments showed that this had no appreciable effect on the determination. No difficulties in using this method were encountered. It was found that both the Winkler's solution and the N/10 sodium thiosulphate kept well in the hot climate.

Phosphate-content.—In this estimation several difficulties arose. The method used was that of Déniges (6), modified by Atkins (2). Ammonium molybdate and tinfoil were taken out in weighed quantities. Standard phosphate was also taken out, but it was found necessary to make up new solution from the solid phosphate at intervals of about one month. A sample of this substance was brought home at the end of the investigation, and we are indebted for an analysis of it to Mr. A. P. Orr, of the Millport Marine Station. It showed at that time 92 per cent. purity, and the results have been corrected in accordance with this figure. The acids were obtained in Paraguay.

Especially the following difficulties were encountered :—

(1) The solution of stannous chloride, made from the tinfoil and hydrochloric acid, rapidly broke down, probably on account of the high temperature. It was necessary to make it afresh for each set of observations.

(2) The blue colour given by the copper-molybdate reaction was very unstable. It was found necessary to make the standard for comparison of this colour at least once for each set of observations, and sometimes more frequently.

(3) Most of the waters had a marked yellow tint. This made the usual method of comparison of the colours in Heine-tubes impossible. A comparator method was evolved similar to that used in determinations of hydrogen-ion-concentration, but with much larger tubes.

Four similar tubes were used. They were filled thus :—

- (1) A known quantity * of the water to be estimated.
- (2) Rain-water.
- (3) The same quantity of the sample as that in tube 1.
- (4) The standard phosphate-solution.

To the sample of the water to be estimated in tube 1 the reagents were then added. This tube and tube 3 were then diluted equally, until the colour on looking through the two pairs of tubes (1, 2 and 3, 4) was the same. Thus the yellow colour of the water was equally diluted in both pairs of tubes, and did not interfere with the comparison of the blue colour given by the phosphates. The concentration of the phosphates in the original sample could be estimated by the amount of dilution necessary to bring it to the same depth as that of the standard.

In this method the concentration of the reagents in the sample varies as the water is diluted, but it was found that the blue colour was simply diluted so long as the amount of the water added was not too great. This

* Usually 50 c.c.

could be controlled by making the standard of a concentration of phosphates not too far from that of the sample. The method was tested by estimating the phosphates in the same sample of water with standards of different strengths, and thus with varying amounts of dilution. It was found that approximately the same values of the content of the sample were obtained. The largest errors arose from the difficulty of matching the tints by this method, which was not by any means as accurate in this respect as the method usually used. Fortunately, the phosphate-content of the waters was very high and the variations large. The method was therefore sufficiently accurate for the purpose. It is estimated that the observations are correct to 0.5 mgr. per litre.

Penetration of Ultra-violet Light.—This was estimated by the method of Moss and Knapp (7), in which the decomposition of oxalic acid, produced by the light, in the presence of uranium acetate is used to determine the amount of the light. The light measured is mainly that in the ultra-violet part of the spectrum. Weighed quantities of oxalic acid, uranium acetate, and potassium permanganate were taken to South America. The sensitive solution was exposed in quartz tubes of 5 c.c. capacity. When the tubes were immersed in water, it was found necessary to place a thin capillary glass tube through the cork. In this way a path for the escape of the gases, which are given off during the reaction, was provided. If the diameter of this tube was small enough, there was no danger of water from the outside passing inwards to dilute the solution. The method was found to work well, and no peculiar difficulties were encountered.

In many ways all these observations could have been made more accurate under more favourable conditions. Owing to the large variations in all the characteristics of the waters, it is hoped that the observations will serve their purpose of defining the conditions in a tropical swamp of this kind, and the changes in these conditions due to the rainfall and to seasonal changes in the climate of the country.

IV. ATMOSPHERIC CONDITION DURING THE PERIOD OF THE INVESTIGATION.

Records of the daily maximum and minimum readings of the dry-bulb thermometer and of the rainfall during the period of the investigation are given on Pls. 11 and 12*. The records taken at the station also included those of the wet bulb and of the barometer, and estimations of the wind and cloud. These are not published, being of less importance to the subject of the investigation.

* For these data the authors are again indebted to the staff of the Mission

The records are summarized in the following table :—

	<i>Temperature.</i>						<i>Rainfall.</i>
	Average Maximum.		Average Minimum.		Average daily mean.		
1926.	° C.	° F.	° C.	° F.	° C.	° F.	mm.
October ..	35.0	95	17.7	63.9	26.4	79.6	87.0
November .	35.0	95	20.8	69.4	27.9	82.2	176.9
December..	34.7	94.5	21.4	70.5	28.0	82.4	92.6
1927.							
January ..	37.3	99	22.2	72	29.7	85.5	146.6
February ..	38.1	101	20.9	69.6	29.5	85.1	14.1
March	36.5	97.7	21.7	71.1	29.1	84.4	99.7
April	31.8	89.2	17.9	64.3	24.8	76.6	215.8
May	27.8	82	14.9	58.8	21.4	70.6	42.6
Average for six summer months (Oct.-Mar.).	36.1	97	20.8	69.4	28.4	83	
Total rainfall for six summer months							726.9

A comparison of these figures with those of the averages over several years given above (p. 216) shows that the summer was hotter and drier than the average. This came at the end of a previous period of six months of dry weather, and produced a considerable drought at the end of the summer. At this time (March) the swamps at Makthlawaiya dried completely.

The weather of the period of the investigation was different in type in three successive periods. During the months of September, October and the first part of November, there was little rain, and the temperature was very variable. By the middle of November the weather had taken on the type which it retained throughout the summer months. The maximum temperature lay generally between 30° and 40° C., but sometimes exceeded the latter figure. The minimum lay around or slightly above 20° C. There was rain every three or four weeks until the end of January, but February and March were very dry months with only one considerable fall of rain. The temperature did not fall greatly until the end of March.

In April and May the weather was again variable with large variations of temperature. In this respect it was similar to that of the early months of the period. The month of April was by far the wettest month of the seven. The greater part of its rain fell on four successive days towards the end of the month. This rain (169.6 mm.) was sufficient to refill the swamp, partly with water draining off the neighbouring land and partly with flood-water flowing over the land from districts further to the west. Thereafter, until the investigation was closed at the beginning of June, very little rain fell.

The highest temperatures were always accompanied by the northerly wind and a comparatively dry atmosphere. Evaporation was intense on these days, and was increased by the great strength of the wind at midday. As a result of this, when the dry bulb was standing at 40°–44° C., the wet bulb comparatively rarely rose above 32° C. and never above 36°. This was of importance to the life of the swamp in keeping the temperature of the water lower than it otherwise would have been. In the early morning the difference between the two bulbs was never greater than 4°–5° C., and dew was frequent, especially during the hot months.

V. DESCRIPTION OF THE LOCALITIES AT WHICH THE OBSERVATIONS WERE TAKEN.

The central station of the Mission at Makthlawaiya (see above, p. 216) is placed on an island surrounded on all sides by lower ground, most of which in wet weather is covered with swamps. The greater part of these were dry at the time at which the investigation was started, owing to the period of dry weather in the preceding six months. On one side of the station a dam had been made across the swamp, with the object of retaining water for the use of cattle. Here there was still a typical swamp. It was also close to the laboratory at the station. It was therefore here that most of the observations were made.

It seemed clear that continuous series of observations at a few selected points would be of more value than scattered observations taken indiscriminately in various parts of the swamp. Several places which seemed to give a sound idea of the range of conditions were therefore chosen and used as observation points. In all there were eight of these in the swamp, but two—one near the edge and one in the centre among the clumps of tall plants—were chosen for the most complete series of observations. These are called A and B in the following description. Scattered observations were also made throughout the period of the investigation in other parts of the swamp, and in any other waters which were found in the country. The result of all these observations was to show that no other types of environment than those exemplified by the two chief observation-points occurred in the swamps. In the following discussion, only the observations at these two points will be considered, but the evidence in our possession is much broader than that given here, and indicates that the conclusions reached apply generally to the swamps of the country. The necessity for compression forces us to restrict the discussion to these two points.

It was clear at once that most of the planktonic life of the swamp and most of its fishes were to be found in the open area around its edges. The chief observation point in this area (A) was at a place where the presence of

small open pools would allow the effects of the floating blanket of vegetation, which elsewhere covered the water, to be determined. Fig. 3 (Pl. 9) is a photograph of a view over this part of the swamp, and a closer view of the floating vegetation is given in fig. 6 (Pl. 10).

There was a varied fauna among the roots of the floating plants at this point, but it was never very numerous in individuals. It included almost all the groups of freshwater animals, among which insects, copepods, cladocerans, rotifers, and fishes were the most numerous. An amphipod, *Hyalella* sp., was very common. The aquatic flora was slight: a few *Volvox* were to be found and various green algae. This fauna and flora persisted until the swamp was almost dry, without much variation except in numbers. In the open pools life was very scarce. In the mud at the bottom of the water only a few small *Oligochaetes* (*Aulophorus* spp.) were found. The variations of the fauna and flora in this and in other waters of the country will be more fully described in a later paper.

The point at which the conditions in the central region of the swamp were to be investigated (B) was chosen near the middle of the dam, which crosses the swamp in this neighbourhood. It was in the centre of the area of the clumps of tall plants, and at this point the water was as deep close to the dam as anywhere in the swamp. It was therefore a conveniently accessible point at which the conditions in the centre of the swamp could be investigated.

Here and everywhere among the clumps of tall plants there was very little truly aquatic life during the hot weather. As a rule, no animals or plants were to be found in the clear yellow water around the stems of these plants. This was always so where the clumps were crowded, but in places near the edge of the part of the swamp filled by them, and in small open pools in this region, the water contained a fauna very similar to that of the outer part of the swamp. After the heavy rain of April, this fauna extended into all parts of the swamp, and was as plentiful among the roots of the tall plants as elsewhere.

After rain large areas of the plains are covered with water to a depth of 2, 3, or more inches. Within a few days this drains off into the swamps and streams. It is obvious that no connected series of observations could be made in water which was on the ground for so short a time. The only other types of natural fresh water in the country are the streams and small pools in the open plains and in the woods. The investigation of the waters of the streams would have been very interesting, but unfortunately there were none within several miles of the station. For this reason an investigation of this type of water would have involved too great an expenditure of time. Two pools in the open pasture, different from each other in general characteristics, were chosen for special investigation and for comparison with

the swamps. Observations were also made in three other pools, but less consecutively. They lead to no different conclusions, and they will not be discussed.

The first of these two pools (C, Pl. 10. fig. 7) was a low-lying spot which in dry weather was covered with grass similar to that of the land surrounding it. After rain, water collected at this spot and formed a pool, 10 × 12 yards in area and 2 feet deep. It lay on the course of the main drainage of the surrounding land, so that much water passed through it during rain. At the end of a heavy storm its contents were, therefore, much more nearly pure rain-water than any of the other waters investigated. The bottom of this pool was a peaty soil filled with roots of the grass. Its water was always clear. Whenever there was water in it, this pool had a crowded fauna of branchiopods, copepods, cladocerans, vorticellids, aquatic insects, and many other forms. Its water was often densely filled with large colonies of *Volvox*. Two or three weeks of hot weather were sufficient to dry it after it had been full.

The other pool (D, Pl. 10. fig. 8) was smaller and deeper. It was circular, 4 yards across and 3 feet deep. It occupied a hole in the ground from which earth had been dug. The bottom was grey mud above clay and the water often cloudy. Its fauna and flora was as numerous in individuals as that of the other pool, but much more restricted in type. Copepods, cladocerans, and *Volvox* were predominant forms, and were often present in very great numbers. In both pools the fauna was much richer than was ever the case in the swamp. This pool evaporated more slowly after rain, but was usually dry after a month of rainless weather.

VI. OBSERVATIONS AND ANALYSES.

(1) *The Outer Region of the Swamp.*

The observations made at the position A in this part of the swamp are summarised on Pls. 11 and 12. When the work was commenced, there was an open pool here, and a large area surrounding it covered with floating vegetation. By November 10th the vegetation had completely covered the water, obliterating the pool, and the area continued in this condition until the swamp dried in March. So long as the pool remained, observations were taken both in it and among the floating weed. Those made in the pool were not sufficiently continuous to be included in the charts, and will be mentioned in the following discussion. All the records given in the charts were made among the floating weed.

The depth of the water is recorded on the lower part of the charts. It will be seen that it varied regularly with the rainfall, and that, if variations of short period are neglected, it remained at about the same level until the

middle of February. During that month the depth decreased rapidly. The area dried shortly after this. It was again flooded by the heavy rain of April, but the floating plants had died while the area was dry, and the water was open or covered only with *Lemna* and small quantities of the water-ferns until the end of the period. After April 23rd flood-water was flowing into the swamp and the depth increased continually. Shortly after this the water was deeper than it had ever previously been. At this time observations were taken in the area covered with *Lemna* and at a neighbouring position among the clumps of tall plants.

Several analyses of water from this position are given in Appendix II. No evidence was obtained that the variations in these characters were of importance to the fauna.

The conditions in the water before the swamp dried in March will be first discussed.

(a) Conditions during the Summer (October–March).

Temperature.—The temperature of the mud at a depth of 6 in. is given. It showed very slight variations from one day to the next and from morning to afternoon. These were never greater than 1°C . on any one day. During the summer months the temperature of the mud remained constant at 23° – 25°C ., and was usually slightly higher than the minimum temperature of the water. This fact indicates that most of the cooling of the water at night was from the surface (p. 228, below). The temperature of the mud rose rapidly in February and March, when the layer of water above it was very shallow.

The minimum temperature of the bottom water was always identical with the minimum at the surface, and is not given separately on the charts. The daily range of temperature on the bottom was not less than 3° – 4°C . That of the surface water was much greater, and sometimes as much as 15°C . or even more. There was thus a large difference of temperature between the layers of the water at midday. Observations to be recorded below show that the water altered most in other characteristics at a depth of about 4 in., and this was also true of the temperature. It seemed that the water could be divided into an upper layer of this depth in which the surface conditions were dominant and a lower layer of much more stable conditions—in fact, that during the daytime there was a thermocline at this depth. It will be shown that this persisted, except in temperature, at night. In the open pools in this area the difference in temperature between the upper and lower layers of the water was less than among the weed, but only slightly so on calm days.

Alkali-reserve (Bicarbonate-content).—The concentration of bicarbonates varied regularly with the rainfall and the evaporation of the water, being

less when the water was deep and increasing as it evaporated. This was to be expected, but that the concentration was not solely to be accounted for in this way was shown by the fact that when the swamp was low the value was always smaller than the evaporation of the water indicated. Some other factor was also at work, perhaps the action of the flora and fauna in fixing bicarbonates in their tissues.

No variation was observed between the different parts of the area in this factor at any one time.

Hydrogen-ion-concentration.—These waters, and most of those investigated in the Chaco, showed very little variation in this factor. The reaction was slightly more alkaline when the water was shallow (pH 6·8–6·9), and more acid when it was deep after rain (pH 6·2–6·4). Occasionally small diurnal variations were found to occur, but these never exceeded pH ·05. They occurred chiefly among the weed. The smallness of these diurnal variations in the water of the swamp was clearly due to the fact that almost all the vegetation was aerial. Large diurnal variations in the Chaco were usually associated with the presence of *Volvox* in great quantities, and it has been stated that it was only occasionally present in the swamp and always scarce. The surface and bottom layers of the water also differed very little in reaction, never by more than pH ·05.

Carbon dioxide-content.—The concentration of carbon dioxide in the swamp water was very great, even when the fact that the method used estimates the whole amount present in all forms is taken into account. It was at a minimum after rain. The water then contained 30–40 c.c. per litre. In a few days the value rose to 50–70 c.c. per litre. This may be regarded as the normal value for these waters. It did not rise further until the water became very shallow, but as much as 100 c.c. per litre were found to be present when the swamp was nearly dry.

Owing to the large amount of carbon dioxide present in the water, variations in the content of this gas caused by the activity of the fauna were necessarily much smaller in proportion to the whole amount present than those in the content of oxygen. They were, in fact, so small as to be almost unrecognizable. This is indicated by the small diurnal variations of pH and alkali-reserve.

More carbon dioxide was usually found in the water of the open pools than among the weed. Both animal and plant planktonic life was much less in the pools. This is therefore, perhaps, not a surprising result.

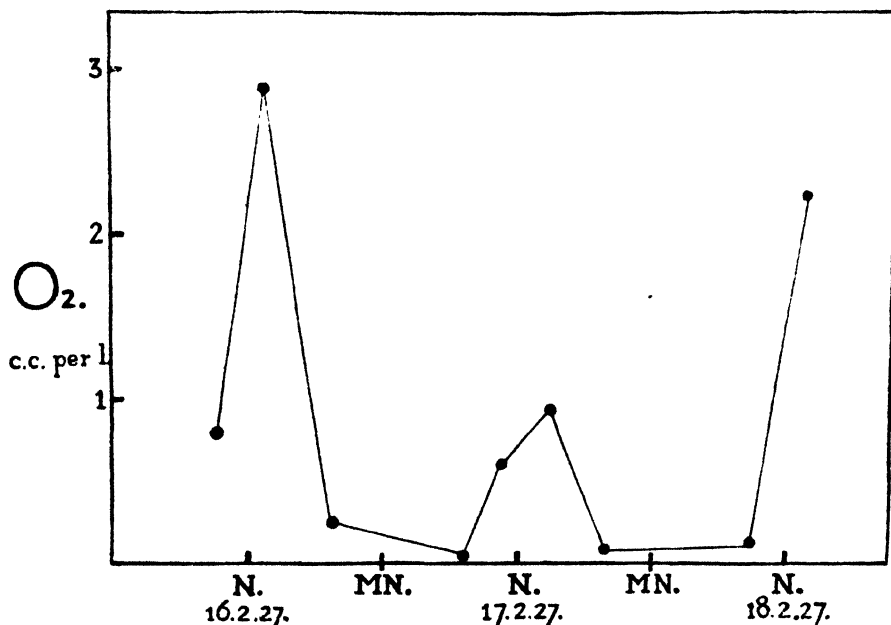
Oxygen-content.—The clearest bionomic results were obtained in the study of this factor. The content of the waters in this part of the swamp varied greatly, but was always small. There were considerable diurnal variations.

In the *surface layer among the weed* * the content was especially variable,

* The samples of the surface water were always taken within half an inch of the surface.

both from one position to another and in time. At the same time, 2-3 c.c. per litre was often found in the surface water of small patches of open water a few inches across, and no measurable amount in the water close to the leaves of the weed and among their stems. Frequently a measurable amount of oxygen (0.02 c.c. per litre) could not be found anywhere, even in the surface water. Thus, between November 15th and 30th the values at the surface were never greater than 0.7 c.c. per litre and usually less than 0.5 c.c. From the 25th to the 27th there was no measurable amount of oxygen in the surface water. During this period there was little diurnal variation. The animal plankton was very scarce and only found near the surface film

TEXT-FIG. 2.



Diurnal variation of oxygen-content in the surface water of the outer part of the swamp.

of the water and among the plants, from which it appeared to derive some oxygen. Again in March, when the swamp was drying up, there was no measurable amount of oxygen in the water.

Nowhere in the water of this part of the swamp did the value of the oxygen-content approach saturation. At the temperature of the surface layer at midday (35°-40° C.) water is saturated with about 5 c.c. of oxygen per litre; at the cooler temperature of the night it could have contained 6.0-6.5 c.c. Values above 2-3 c.c. in the surface layer were rare, and never occurred except immediately after rain. During hot and calm weather the oxygen-content of all parts of the water fell off.

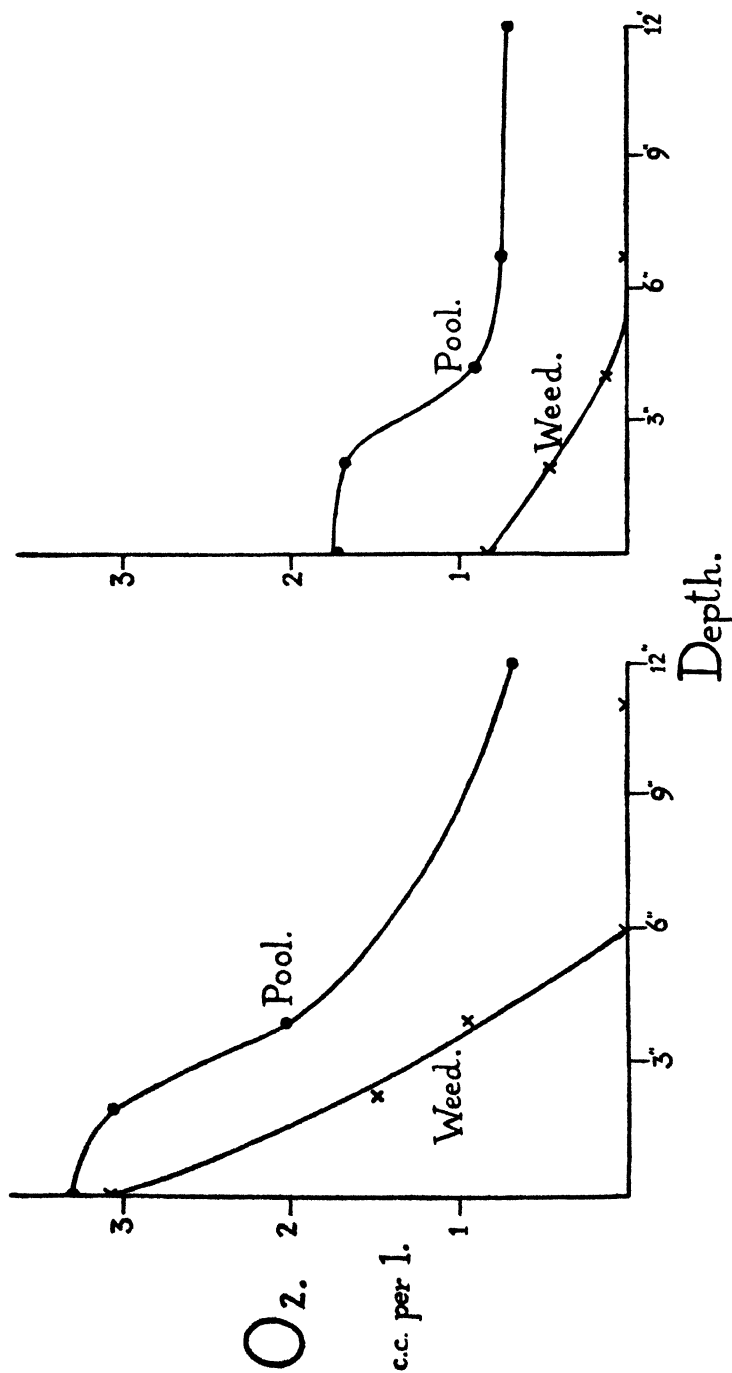
In the water of the open pools in this area there was always more oxygen at the surface than among the weed. 2-3 c.c. per litre was almost always present.

Observations in which diurnal variations in the surface water among the weed were observed are given in text-fig. 2. The variations are here more marked than they usually were. Owing to the large and very local variations of the oxygen-content of the water at the surface it was difficult to be certain of the size of these diurnal variations.

When the *variation of the oxygen-content with depth* was studied, a great difference was found between the water of the open pools and that among the weed. In the latter it was the rule to find no oxygen in the lower layers of the water. Only occasionally as much as 1 c.c. per litre was found, and values below 0.2 c.c. per litre were far more common. Most commonly no measurable amount of the gas could be found in the water. These conditions extended to within about 4 in. of the surface. In the layers above this the content rose rapidly to the surface value. In the pools the content fell more slowly with the depth, and there was always a considerable amount of oxygen in the bottom water. Typical observations, taken on days on which the amount of oxygen in the surface layer was high, are given in text-fig. 3.

The higher value of the content in the lower water of the pools was clearly due to greater disturbance caused by the absence of the floating layer of weed. The distribution of the oxygen in the layers of the water among the weed and the temperature gradient in this water in the daytime show that it was almost always entirely undisturbed. This was so even when a strong wind was blowing. On some of the rare occasions on which oxygen was found in the water below the weed it was noticed that the previous night had been cool. This raises the question of mixing of the layers due to cooling of the surface at night. It has been stated above that the temperature of the top and bottom water was identical at dawn, but this does not necessarily imply that the layers were always mixed. So long as diffusion of heat during the cooling was sufficient to maintain a gradient from warmer water above to cooler below, no mixing would occur before the whole of the water became identical in temperature, and it would not take place then if the water was not further cooled. Our observations seemed to show that mixing took place when the night was cool (a minimum air-temperature of about 15° C.). It would occur more readily if the maximum temperature of the water at the surface on the previous day had been low, for less cooling would then be required to bring the two layers to the same temperature. Reference to the chart will show that, on the occasions on which oxygen reached the lower water among the weed, the maximum of the previous day was usually low. Thus on December 14th a

TEXT-FIG. 3.



Oxygen-content of the water in the outer part of the swamp.

low maximum and a cool night were followed by an increase in the oxygen-content of the lower water, but on January 5th an even cooler night with a much higher previous maximum had no such effect. It would seem that mixing due to this cause occurs regularly in temperate waters.

One cause of the lack of oxygen in the lower layers of these waters is, therefore, the absence of disturbance of any kind. Only when the night is cool, and perhaps during exceptionally heavy rain, or when the swamp is flooded with water from the outside, can oxygen reach this water otherwise than by diffusion through the layers above it. The normal rainstorms, however, often produced no such effect. The other conditions which help to produce the shortage of oxygen in these waters will be discussed below.

Phosphate-content.—In the waters of this part of the swamp the phosphate-content was very high (1.4–4 mgrs. per litre). It was fairly constant, but there was some evidence that the content was greatest when the swamp was full after rain. There was certainly no increase in the concentration as the water evaporated. On the contrary, the content was at its lowest when the swamp was nearly dry in March. Probably this points to the conclusion that the main source of the phosphate supply of these waters is from the land. In corroboration of this it may be noted that the flood-water which reached the swamp in April, after flowing over the land for many miles, was very rich in phosphates (3–7 mgrs. per litre). It is clear that the land is not the only source of phosphate. Much must also be derived from the decay taking place at the bottom of the water.

The high concentration of phosphates (100 times that of sea-water) excludes the possibility that the fauna suffers from starvation in this respect.

(b) Conditions during April and May.

The conditions in the water of this part of the swamp after the heavy rain of April are shown on the right-hand part of Pl. 12. Analyses of the flood-water on three different days as it flowed into the swamp are also given. It will be seen that this flood-water was very similar to the water of the swamp at times at which it previously had been high. Its reaction of pH 6.7 was nearly the same. The alkali-reserve and the carbon dioxide-content were low, but not lower than had sometimes been observed in the swamp-water. Only the phosphate-content was different, being higher than it had ever previously been. This water contained a very plentiful plankton. Chemical analyses of it are given in Appendix II. The oxygen-content of the flood-water was not estimated.

Soon after the flood-water began to flow into the swamp, the water of the swamp became identical with it in respect of all the characteristics investigated. The conditions in the swamp at this time therefore contrast strongly with those just before the flood-water reached the swamp, and also with those just before it dried in March.

The oxygen-content of the water of the swamp after it had been flooded was not very different from that of the same water during the summer. There was, however, rather more oxygen in the lower layers, as much as 1 c.c. per litre being often found. This may have been due to greater disturbance, caused either by the thinner layer of floating weed or by the cooler nights. Much oxygen in these waters must have been absorbed by the activity of decay at their bottom. It is possible that the cooler temperatures of May and June allowed more oxygen to remain in the water by reducing the activity of the processes of decay.

In general, the conditions of the water at this time were less distinctly tropical than they had previously been.

(2) *The Central Region of the Swamp.*

Among the clumps of tall plants which everywhere fill the central region of the swamp, the nature of the environment was in many ways different from that of the water at the edge of the swamp. The clear yellow water, poor in animal and plant life, which surrounds the stems of these plants is in heavy shade from the thick vegetation above it, and is completely protected from the action of the wind. It is stagnant, but never foul.

Many analyses of the water in this part of the swamp were made. They were taken at the position B near the centre of the dam crossing the swamp (p. 222) and at many other places. Inorganic analyses of the water are given in Appendix II.

The results of these observations may be summarized as follows:—

(1) The temperature conditions were similar to those in the outer region of the swamp. There was always a large fall of temperature from the surface towards the bottom in the daytime and hardly ever any mixing at night by convection.

(2) The alkali-reserve was very variable in amount, but was always in excess of the quantity in the water of the outer region at the same time. Usually the values were 50–100 per cent. higher. Occasionally very high values of alkali-reserve were found to occur (·003–5 N.). These were usually in water which was very shallow. It was interesting to find that the fauna appeared to be unaffected by this large range of variation.

(3) The pH was almost the same as in the outer region of the swamp (pH 6·3–6·7), so long as the alkali-reserve did not rise above ·003 N. Where the concentration was higher, the water became more alkaline, and values as high as pH 7·2–7·4 were observed. It seemed that the variations in pH had no more effect upon the fauna than those in the alkali-reserve.

(4) In accordance with these values of the reaction and of the alkali-reserve, the amount of carbon dioxide in the water was very great and always greater than that in the outer region of the swamp. Usually from 60–100 c.c. per litre were present and, most commonly between, 70 and 90 c.c. Occasionally as much as 200 c.c. was observed in very shallow water.

(5) The phosphate-content was even higher than that in the outer region. The water usually contained 5–6 mgrs. per litre, and sometimes as much as 10–11 mgrs.

(6) The distribution of dissolved oxygen in these waters was as striking as in the outer region. In the hot weather there was hardly ever a measurable quantity of the gas, even in water collected as close to the surface as possible. Never more than .2–.3 c.c. per litre was found in the surface water, except immediately after rain. In the lower layers of the water it was always entirely absent.

Here, as in the other parts of the swamp, the water was greatly diluted by the heavy rain which fell in April. The conditions then approached those of the outer region much more nearly. The alkali-reserve fell to .0007–.001 N., and the carbon dioxide-content to 30–40 c.c. per litre. The phosphate-content and the reaction were not much altered, but were about the same as those of the water of the outer region at the time. Perhaps, for the same reasons as elsewhere, more dissolved oxygen was present in the water. 0.3–0.5 c.c. per litre was found in the lower layers of the water, and as much as 1–2 c.c. in the surface layers.

It has been stated above that this alteration in the conditions was accompanied by a great increase in the fauna, which was also very similar to that of the outer region of the swamp.

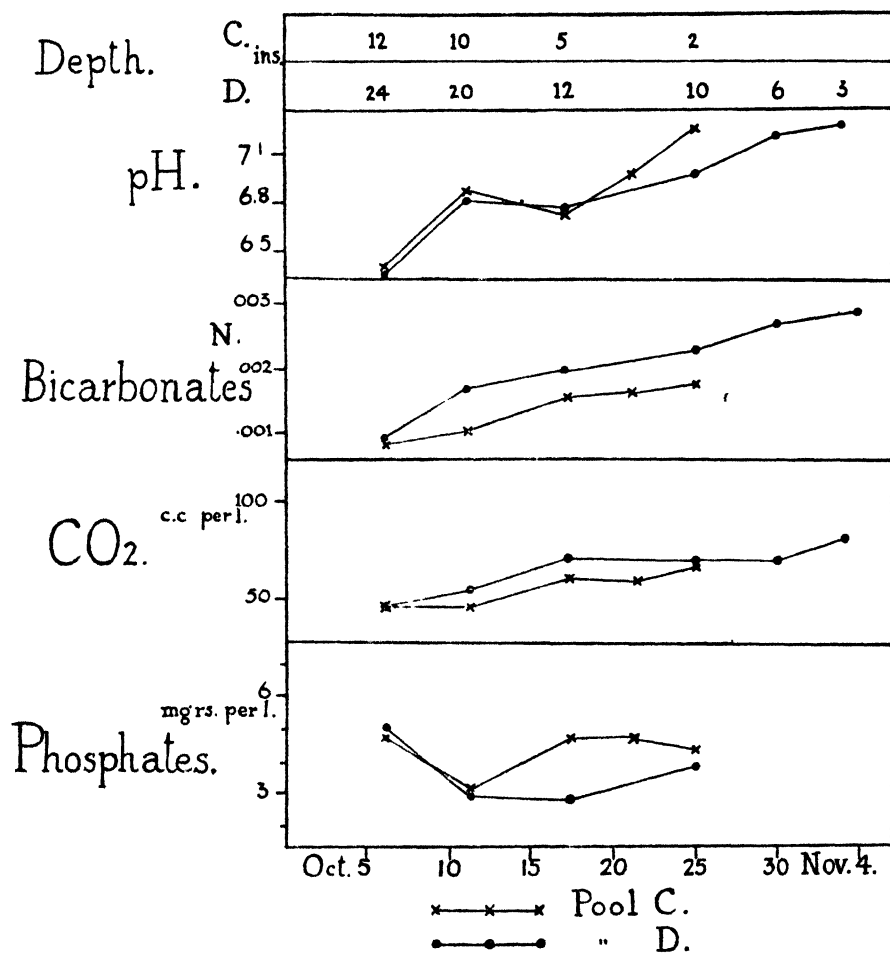
(3) *The Rain-water Pools (C and D).*

Open pools such as these, which are filled by each storm of rain and dry in a period of three or four weeks of hot weather, present a different subject for investigation from that of the more or less permanent waters of the swamp. In them the bionomic cycle is not seasonal, but from one filling of the pool to its next drying-up. Often this cycle is incomplete; the pools are refilled before evaporation has completed its work. It is clear that under these circumstances it will be less easy to unravel the effects of the various changes in the conditions of the water. The most favourable time for investigation will be an occasion on which the full cycle is passed through. The best example of this occurred in October 1926, when the pools were filled with water by the rain at the beginning of the month, and dried without any considerable further rainfall—C on November 26th and D on November 2nd. The results of observations made on the pools at this time are given in text-fig. 4. Observations were made continuously during the period of the investigation, but lead to no different conclusions.

The pools were full after the rain, but the surrounding land was not much flooded. As a result, chemical substances dissolved from the soil were not washed away by the streams flowing through the pools, and their water was from the first much more different from rain-water than after heavier

rain on several occasions later in the year. In the latter part of the summer, on one occasion the water of the shallower pool (C), through which the stream was greater, had an alkali-reserve of $\cdot 00029$ N. At the same time, that of the deeper pool was $\cdot 00048$ N. The earliest values recorded in the

TEXT-FIG. 4.



Variation in the waters of the two pools with evaporation.

figure are considerably higher than this ($\cdot 00069$ and $\cdot 00098$ N.), but the changes during the cycle were similar in all cases.

Inorganic analyses of the water of these pools are given in Appendix II.

It has been stated above that the water of the shallower pool (C) was always clear. As a result of this, the penetration of ultra-violet light into its water was always much greater than into any other of the waters investigated (p. 224). It was therefore not surprising to find that plant-life was active

in all layers of the water of this pool in the daytime, and that diurnal variations were large in all the layers. In the other pool the water was always somewhat cloudy, and became more so as evaporation went on. Light penetrated its water to a much less extent, and the diurnal changes only occurred in the upper layers of the water. This difference between the two pools was made more obvious by the absence of disturbance in the pool D, due to its depth and the shape of its banks; but it was only on windy days that the water of the other pool was completely mixed.

The large diurnal variations to be recorded below made the comparison of observations taken over several days difficult. The observations from which text-fig. 4 is derived were all made in the morning between 9 and 10 A.M., and are therefore as comparable as it seemed possible to make them; but variation of the weather was bound to introduce irregularities into the results. To this cause the unevenness of the curves is probably due.

It will be seen from the figure that there was a continuous and fairly constant rise in the alkali-reserve of the water of both pools during the cycle. It has been stated that the rise in the concentration of alkali-reserve in the swamp-water was not proportional to the evaporation of the water (pp. 225, 232). This was much more clearly true of the water of these pools. In the deeper pool (D) the value of the alkali-reserve increased threefold ($\cdot 00098$ – $\cdot 0028$ N.) as the depth was reduced from 24 in. to 3 in. The water must therefore have been concentrated at least eight times, and probably much more, if account is taken of the sloping of the banks. There was no possibility of the escape of the water of this pool over the land except when it was full, and the impermeable clay layer, which was very close to its bottom, would have prevented any percolation of the water downwards. It seems, therefore, that the concentration of the alkali was in some way prevented, perhaps by the action of the flora and fauna.

The results show a considerable rise in the pH value of the water of both pools as the cycle progressed. It will be seen that the changes in reaction were much greater than occurred in the water of the swamp.

There was also a considerable increase in the amount of dissolved carbon dioxide in the water. Although the pH value was not constant, the amount of carbon dioxide was found to bear a definite relation to the value of the alkali-reserve, and this relation was the same in both pools. Corresponding values are given in the following table. The meaning of this relation is obscure :—

<i>Alkali-reserve.</i>	<i>Carbon-dioxide</i>
Below $\cdot 0005$ N.	10–30 cc. per litre.
$\cdot 0005$ – $\cdot 001$ N.	30–40 "
$\cdot 001$ – $\cdot 002$ N.	40–60 "
$\cdot 002$ – $\cdot 003$ N.	60–80 "

These values of carbon dioxide-content are approximately equivalent to those found in the water containing the same concentration of alkali-reserve from the swamp.

The phosphate-content was as high as in the swamp-water, and sometimes higher. As much as 6-7 mgrs. per litre were observed. From time to time the amount of phosphate in the water of these pools varied greatly, but so long as no rain fell the content often remained approximately constant. This was so in the observations recorded in text-fig. 4. It appeared that the phosphate-content of the water of the pool at the beginning of the cycle depended on that of the rain-water which filled the pool, and this upon such conditions as the amount of rain which had flowed off the land in a short time previously. Here, as in the swamp, there was no concentration of phosphate with the evaporation of the water. Again, the source of the phosphate seemed to be mainly from the land.

The diurnal variations in oxygen-content were so large that it was impossible to construct curves of any value showing the amount present in the water throughout the cycle.

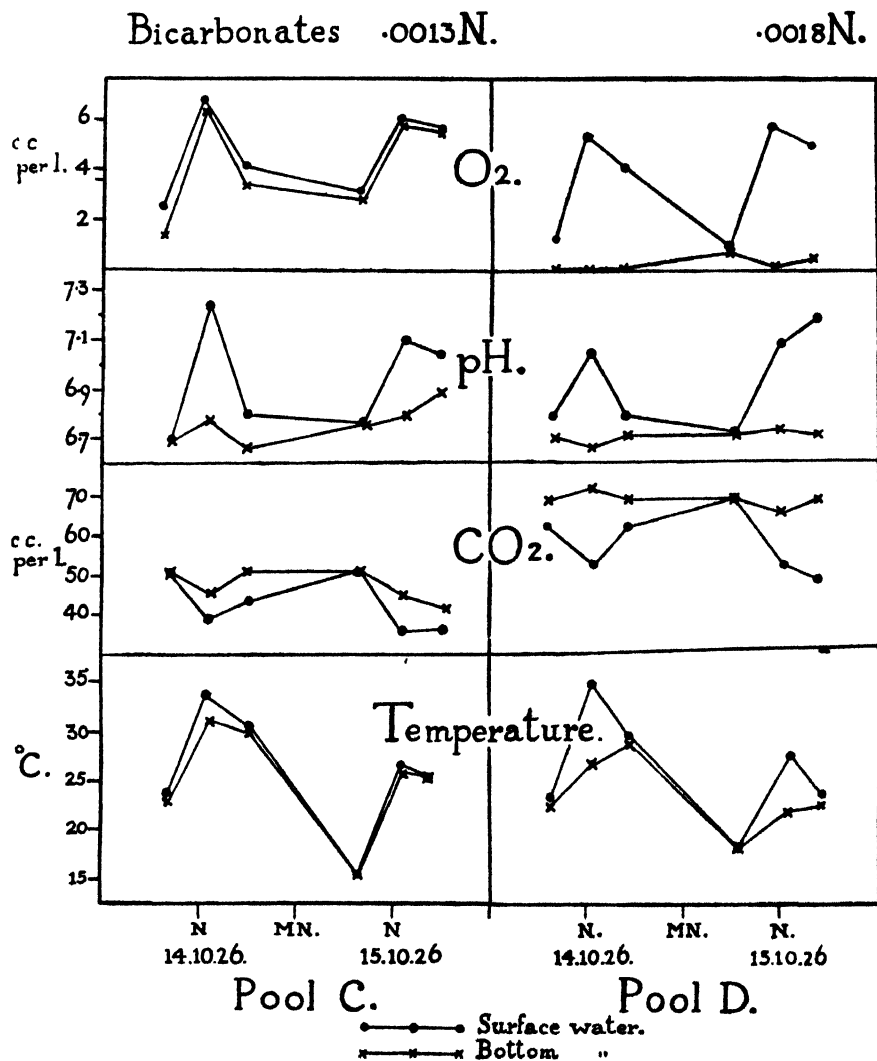
The *diurnal variations* in the water of these pools are shown in text-fig. 5. In it observations taken three times a day on two successive days are recorded. Both days were clear and sunny, but on the second a slight southerly wind was blowing and the atmosphere was much cooler. The temperature of the water of the pools was therefore much lower on this day. It will be seen that this wind was not sufficient to mix the layers of the water of either pool.

These results illustrate the differences between the two pools. It will be seen that the absence of disturbance in the deeper pool (D) and its greater depth prevented the lower layers of its water from receiving so much heat during the day as those of the shallower pool. There was therefore a much greater difference of temperature between the layers of water in the shallower pool. The results also show the higher temperatures which planktonic fauna is able to endure. In the pool D the plankton is forced by other conditions (*e.g.*, the distribution of light and oxygen) into the surface layers of the water at midday. It did not appear to be harmed by the temperature at the surface, even when this rose to a higher point than that recorded in the figure. It was sometimes found to reach 40°-42° C. The limit of life with regard to temperature in these waters will be further discussed below (p. 245).

The figure shows that the diurnal variations in oxygen-content were particularly large. The surface water of both pools was supersaturated in the afternoon, containing as much as 5-7 c.c. per litre. In the shallower pool (C) all parts of the water contained much oxygen, less at dawn than at

midday, but always more than 2.5 c.c. per litre. There was little difference between the layers of the water in this respect. In the other pool (D) the minimum even in the surface layer was lower (less than 1 c.c. per litre),

TEXT-FIG. 5.



Diurnal variations in the water of the pools.

and in the water at the bottom there was never more than 0.7 c.c. per litre, and usually less than 0.2 c.c. In the deeper water of this pool there was practically no diurnal variation, owing to the concentration of the plants on the surface during the daytime,

The variations in the other factors were in accordance with these. Owing to the large amount of photosynthesis in the water, the changes in the carbon dioxide-content were easily measurable. The variations were as great as 15–20 c.c. per litre, and much greater than would correspond to the changes in oxygen-content. It is clear that much of the dissolved oxygen from the supersaturated water must have escaped to the atmosphere. There is therefore no reason to think that these results conflict.

The variations in the pH value were large, and it is perhaps astonishing to note that the fauna, even at the surface of pool D, seemed to be in no way affected by these large and sudden changes in the water.

VII. THE PENETRATION OF ULTRA-VIOLET LIGHT INTO THESE WATERS.

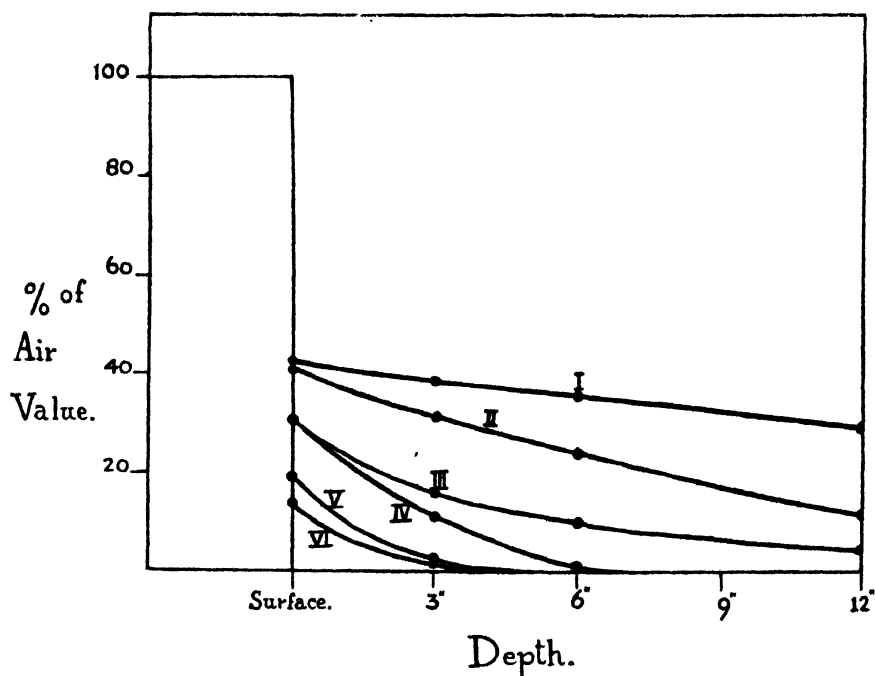
The observations to be recorded in this section were made with the object of testing the possibility that the habits of the fauna might be influenced by the amount of the ultra-violet light in the water, and not primarily to give an estimate of the amount of light available for photosynthesis. In measuring mainly the light at the ultra-violet end of the spectrum, the method is suitable for the former purpose but not for the latter, for which measurement of the red rays are required. It is clear from the work of other authors (*e.g.*, Bertel (3) on the penetration of light into the sea) that light of different wave-lengths penetrates very differently into water. It must be concluded that results obtained with light of one part of the spectrum can only be extrapolated in a most general way to that of another part. Bertel found that blue light penetrated farthest into sea-water, red much less, and ultra-violet less than red. It is therefore probable that the red light needed for photosynthesis will penetrate the waters farther than the ultra-violet was found to do.

Estimates of amount of ultra-violet light at various depths of different waters are given in text-fig. 6. In each case the measurements were made in perfectly calm water at or near midday and at about the same time of the year (April and May). The tubes were exposed attached to a stake, (1) in the air above the water, (2) below the surface of the water and within half an inch of it, and (3) at various depths of the water. They were inclined at about 5° to the horizontal and at right angles to the incident light. They were exposed for one hour. For purposes of comparison the estimations have been reduced to percentages of the ultra-violet light in the air above the water. The experiments on rain-water (curve I) were done in the large iron tank at the laboratory, and may give somewhat too high results owing to reflection from the sides of the tank. All the other estimations were made in the natural waters, and should therefore give true values of the amount

of ultra-violet light in these waters. Care was always taken to avoid loss of light by shading of the tubes.

The estimations give the expected result that the clear water of the shallow pool (C, curve II) contained the most light. Almost as much light crossed its surface as that of rain-water. Below the surface, absorption was slightly greater, but this may have been due to the large amount of plankton in the water. The ultra-violet light which passed the surface of the other pool (D, curve III) was only three-fourths of that in this pool, and in its somewhat cloudy water absorption was much more rapid. As a result

TEXT-FIG. 6.



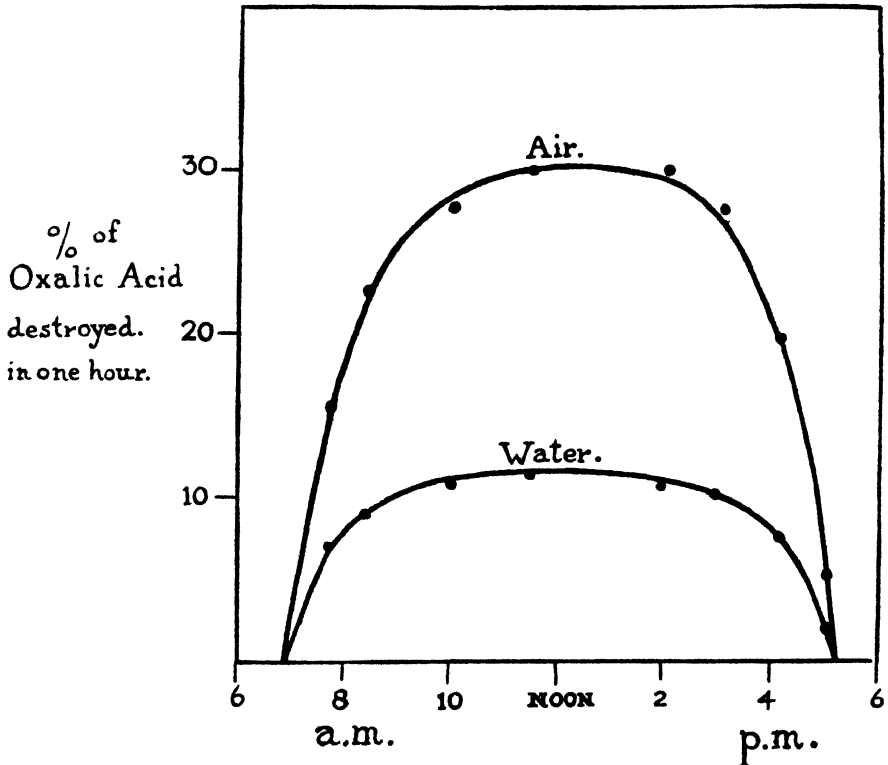
Penetration of ultra-violet light in various waters of the Chaco.

only 10 per cent. of the ultra-violet light was found to penetrate to a depth of 6 in.

The results on the water of the swamp fell into three classes, to which the curves IV to VI given in the figure relate. Everywhere the swamp-water was yellow. It was clear except in some places in the open region at its edge. The yellow colour was much stronger among the clumps of tall plants in the centre of the swamp than elsewhere. The penetration of the ultra-violet light was greatest in the less yellow and clear water among the floating vegetation in the outer region of the swamp (curve IV). The amount of ultra-violet light which passed its surface was the same as

in the deeper pool (D), but absorption below the surface was more rapid, and only 2 per cent. of the light penetrated to a depth of 6 in. The penetration into the cloudy water (curve V) was far less than in any of the previous waters. Not more than one-half as much ultra-violet light passed the surface as in the pool C, and absorption was very rapid. No measurable amount was found at a depth of 3 in. (less than 1 per cent. of the air value). In the yellower water in the centre of the swamp (curve VI) the penetration was about the same as in the cloudy water. It is clear from these results

TEXT-FIG. 7.



that the penetration of ultra-violet light is as much influenced by the colour of the water as by the amount of suspended matter present.

The results were all obtained in unshaded waters. By far the greater part of the water of the swamp is heavily shaded either by the clumps of tall plants or by the floating weed. The amount of ultra-violet light in the water will therefore be much less than is recorded in the curves.

The results of a series of observations of the amount of ultra-violet light passing the surface of a shallow and clear rain-water pool at different

hours of a single day are given in text-fig. 7. It will be seen that the amount of light in the water remains about constant at its highest value from 9 A.M. to 3 P.M., but falls off rapidly outside this period. Very nearly the same proportion of the ultra-violet light in the air was found to penetrate the surface throughout this series of observations, but it was perhaps somewhat less before 8 A.M. and after 4 P.M. When these observations were taken the sun rose at 6.30 A.M. and set at 5.30 P.M. Its height at midday was 54° .

There was no evidence, except possibly in the clear water of the pool C, that the ultra-violet light had an adverse effect on the fauna strong enough to determine its behaviour. In this pool and everywhere else the phytoplankton was concentrated at the surface at midday, but, of the zoo-plankton, the copepods were at that time more numerous at the bottom. Other conditions have been shown above to have been different in the various layers of the water of this pool at midday, but similar variations in other waters did not determine the movements of the fauna. There seems to be evidence, therefore, that ultra-violet light was here the controlling factor. It can be definitely said that it had no controlling effect elsewhere. In the pool D, where all the plankton was concentrated on the surface, other conditions were dominant. In the swamp there was no evidence of an excess of ultra-violet light driving the fauna from the surface. These observations refer to the whole period of the investigation, and not merely to the days on which the amount of ultra-violet light in the water was determined.

It must be concluded that, in the climate of the Chaco, 40 per cent. of the ultra-violet light of the air may perhaps be sufficiently toxic to some of the zooplankton to over-ride other factors in determining its behaviour. Less than this amount is certainly not so, and so much light as this only rarely occurs in the water, and never except within an inch or two of the surface.

It has been stated above that these observations do not determine the amount of light available for photosynthesis in the waters. From observation of the phytoplankton, there was no evidence that the amount of light present was above the optimum for photosynthesis. Even in the clear pool C, *Volvox* was concentrated on the surface at midday. It is not easy to see that the other conditions were more favourable for it in this position, and it must be concluded that the larger amount of light was the attractive factor. These results are in contrast with those of workers on the sea (*e.g.*, Orr & Marshall, 8), who find that even in the temperate climate on a sunny day there is more activity in the diatom flora at a depth of 10 metres than at the surface. It must be remembered that very different types of plant are the subject of investigation in these two habitats.

On the other hand, there was good evidence that the amount of light in the water was often below the optimum for the plants. Even in the shallow pool (C), there was a marked concentration at the surface at midday, and, since the light of all wave-lengths in the yellow waters of the swamp and the cloudy water of the pool D must have been much less than in this clear pool, it is obvious that everywhere except in this pool the phytoplankton had less light than the optimum. It is probable that the small amount of light in the waters of the swamp was one cause, but probably not the only cause, of the poverty of the phytoplankton there.

These observations on the intensity of the ultra-violet light on the waters were all comparative. They were not intended to give an absolute measure of the amount of ultra-violet light present for comparison with that in other countries. However, experiments were made in April 1928 at Millport, Firth of Clyde, under conditions as comparable with those of the observation in the Chaco as possible, and showed that the amount of ultra-violet light in the air was approximately the same in the two places, when the sun was at the same height. In both places 20-25 per cent. of the oxalic acid was decomposed in one hour when the height of the sun was 25° - 30° . The greatest decomposition observed in the Chaco was about 40 per cent. in one hour, when the sun was at the zenith. It would seem, therefore, that there is never more than twice the amount of ultra-violet light in the air in the Chaco than sometimes occurs in Scotland.

VIII. GENERAL DISCUSSION.

In considering these results, it must be remembered that the waters of the Paraguayan Chaco only represent a few of the types of tropical freshwaters, and not those most frequently studied. There are no examples among them of the larger pieces of water, such as the lakes or inland seas, which are of sufficient size to bear a fauna whose life is in no way related to the banks or bottom. We are dealing wholly with the littoral region of the freshwater environment. Nor do they include any that are truly fluvial. It has been stated that the streams which drain the country flow through the swamps, but the currents which they cause are too slow to affect the fauna in any other way than by altering the chemical nature of the water. So far as the fauna is concerned, these waters may be considered stationary.

It is no new observation that tropical waters which appear to have a large supply of food-substances, and would be expected to support an abundant fauna and flora, should prove to be comparatively sterile. The recent work which illustrates this point best, and is also closest in the nature of the waters investigated to the subject of this paper, is that of P. van Oye, who studied the conditions in some streams in Java and in the Congo. He found that he was able to classify the streams of the district in Java

in which he was working into two categories. In the hills, there were clear and rapid streams containing a considerable amount of life, most of which was oligosaprobic (green algæ, diatoms, and rotifers). On the other hand, in the plains there were larger and slower streams of more muddy water. These were very poor in life, although the products of decay must have been abundant. In them the only indigenous plankton consisted of meso- and polysaprobic forms. Without undertaking any chemical analyses, he came to the conclusion that the amount of dissolved oxygen present was the most important controlling factor, and that the conditions were largely influenced by the quantity and type of the rainfall. The turbidity of the water was also of importance in controlling the penetration of light.

His work on the Congo (at Ruki) was done on water at first sight very similar to that of the slower streams of Java. It was muddy, but contained a certain amount of planktonic life. Here, again, he found that the rainfall was a factor of great importance to the life of the waters. After rain the planktonic life increased, although the transparency was less. It would seem that here the amount of oxygen produced by the photosynthesis of the phytoplankton was not the controlling factor; but it must be remembered that the rain would produce many other changes besides the increase of turbidity. The increase in the planktonic life was probably due to some of these—in the case of the animal plankton, perhaps, to the presence of more oxygen in the incoming water. In the Congo he was dealing not with different waters, but with the same water at different times of the year, and the changes were necessarily less extensive. The problems discussed and, at least in the case of the Javan waters, the conclusions to which he comes are very similar to those of this paper.

The waters at Makthlawaiya which formed the subject of our investigations were in many ways particularly favourable to their object. At first sight the various types of water appeared very different from one another, and examination showed that in many of their characteristics they were so. In spite of this, it was to be expected that waters within a very short distance of one another should show great similarity in some respects. The climate and the soil were the same for all. It therefore seems probable that many of the characteristics to which particular attention was not paid (*e. g.*, the inorganic chemical-content) would have shown little variation among the different types of water. So far as they go, the results given in Appendix II support this.

Again, comparison between the waters was made more easy by the great similarity of the fauna in all. It was to be expected that some forms should be restricted to a few of the types of water, and this proved to be so (*e. g.*, the Branchiopoda were only found in the pool C); but the great majority of the forms were, so far as could be determined in the field, identical in all

the waters, occurring only in varying numbers and at various times. Thus the observations were made in the main on the same species under different conditions, and the conclusions drawn from them became much more certain.

Further, the weather was on the whole favourable to the investigation. The abnormal heat and dryness of the summer made it possible to investigate the conditions most carefully when the water was low. It is clear that the fauna must suffer most from the dangers of its environment during this part of the cycle, and it is therefore the most suitable time for the investigation of the conditions which control its survival.

It was the life of the fauna of these waters during the summer months (when the conditions were distinctly tropical) that was the chief subject of the research. In the following analysis of the observations the conditions at that time will be mainly discussed, and in the first part of the discussion they alone will be considered.

If, for the moment, the seasonal variations of the fauna in each type of water are neglected, and if the forms which are not truly aquatic (such as the insects, many air-breathing fishes, and the aerial plants) are excluded, the four types of water which were chiefly studied may be put in a series of decreasing fertility, thus:—

(1) The shallow pool (C), in which the plankton was always very rich, both in plants (especially *Volvox*) and in animals.

(2) The deeper pool (D), which contained a rich plankton at most times, but one far less various than that of the shallower pool. *Volvox* was often very plentiful in its water.

(3) The outer region of the swamp (A), in which the zoo- and phytoplankton was various, but comparatively poor in number of individuals.

(4) The central region of the swamp (B), very poor in plankton and often without animals and plants.

In making an attempt to correlate this series with the differences in the environmental conditions, some of the factors which were studied may be set on one side as playing very little part in the control of life in the water. Among these the following three may be certainly included:—

(1) The *Hydrogen-ion-concentration*.—This varied very little, especially in the swamp. Its normal range (pH 6·2–6·9 in the swamp-water and pH 6·3–7·3 in the pools) was far within that which often occurs in fresh water (pH 5–9). It was also on the acid side of neutrality, and it is rather in the alkaline part of the range that animals are sensitive to small changes in reaction. Further, in the swamps there was no evidence that the animals behaved differently as the limits of the range were reached, either suddenly after rain or gradually as the water dried. It has been stated that very large and sudden variations of this factor in the pools produced no effect on the fauna.

That the reaction is not a factor of great bionomic importance in these waters is interesting in view of the large claims which have been made for it as controlling the life of freshwater habitats. This it certainly does in some instances (Wells, Lake Mendota, 15).

(2) The *Alkali-reserve*.—There was no evidence that variations in this factor were of importance to the fauna, except perhaps where the concentration was very high (above .003 N.). Waters which contained so much alkali as this were usually in the last stages of evaporation, and in them many factors, whose effects it was not possible to isolate, were varying at the same time. For instance, with the presence of much alkali was necessarily associated a large volume of carbon dioxide in the water. This may itself have been of importance to the fauna. Certainly, at the other end of the range, the waters with the least alkali-reserve (less than .0003 N.) were no more toxic than those with more. This range of variation is about that normally met with in fresh waters in the temperate zone (2.5 to 25 parts per hundred thousand).

(3) The *Phosphate-content*.—The very large amount of these substances which was present in the water was surprising, and entirely excluded the possibility that a shortage of them might control the amount of the flora and fauna. There was also no evidence that the high concentration of phosphates was toxic. Thus the flood-water, which contained a very plentiful plankton of all kinds, sometimes had a phosphate-content of 7 mgrs. per litre.

The concentration was much higher than is usually found in temperate waters, even of the same type. Atkins (2) never found a higher concentration than 1.2 mgrs. per litre in waters of different types near Plymouth. On the other hand, the Plymouth aquarium sea-water has a content of 4 mgrs. per litre, about the same as that of the waters of the Chaco. Atkins found marked seasonal variations in the phosphate-content of some of the waters which he investigated. The absence of seasonal variations of this type in the tropical waters was striking, but perhaps not surprising in view of the high concentration of the substances. The reduction of the phosphate-content as the water evaporated was probably due to the use of these substances by the animals and plants.

It has been suggested in the preceding pages that much of the phosphate of the water is derived from the land. This is in accordance with the views of agriculturists on the leaching of chemical substances from the land (Russell, 12). In tropical countries the large amount of plant-life which follows each rain, and the decay of much of this material before the next rain, must set free much phosphate in the soil. If this is true, the land acts as a reservoir for the waters of the country in just the same way as the deeper waters of the sea do for those at its surface.

This process must set up a continuous drain on the phosphate of the soil of the higher land, which can only be made good from the subsoil or by the

action of animals. In the Chaco the soil is completely isolated from the underlying silt by the impervious layer of clay. The only obvious source of phosphate in the soil is therefore the action of the animals which may transfer it from the swamps and other low-lying ground. In the swamps much is derived from the flood-water coming from districts to the west, but none of this water reaches the higher ground. In the swamps, also, the decay at the bottom of the water must set free much phosphate.

Probably the following factors may also be excluded, except in exceptional circumstances :—

(4) *The other Food-factors.*—Concerning the supply of these substances (*e.g.*, the nitrates and the nitrites), no direct evidence was obtained. When the large amount of bacterial decay in the waters and the large phosphate-content are considered, it seems very unlikely that sufficient of the other products of decay for the food-supply of the life in the water were not present. The use of these substances by animals requires their previous assimilation by plants. The small quantity of plant plankton in the swamp-water may have restricted the increase of some members of the animal fauna. This will be discussed below. Other animals which feed on aerial plants could not have been limited in this way.

(5) *Temperature.*—For a few hours in the middle of the day the surface water of the pools and of the swamp sometimes reached a temperature of 40° – 42° C. (104° – 108° F.). In none did the average temperature throughout the twenty-four hours exceed 33° – 34° C. (90° – 93° F.), and in all except the shallowest waters the temperature of the lower layers was much below 40° C. at all times. It has been found in the laboratory that the highest temperature at which *Cladocera* from temperate waters will live continuously is 33° – 34° C. (Brown & Crozier, 5). It seems probable that those of tropical waters would be adapted to life at a higher temperature. It was certainly true that the plankton could survive in the waters of the Chaco for a few hours at the much higher temperature of 40° C. This was particularly clear in the pool D, where the plankton was forced into the surface layer at midday by other conditions. It was also observed that Copepoda were active in pools a few inches deep at the edge of the swamp when the temperature was 42° C.

The habits of the fish (*Hoplosternum* (*Callichthys*) *litorale*) show very clearly that some animals are able to endure the temperature of the surface layers of the water of the swamp. This fish lays its eggs in a floating nest of decaying leaves and sticks which it makes on the surface of the swamp. In it the eggs pass through the whole of their embryonic development, and the young larvæ live for some days after hatching. The development is very rapid in association with the high temperature, and the whole of the stages in the egg are passed through in three days. The temperature at which these larvæ live must often reach 40° C., and perhaps be even higher owing

to the heating of the nest by decay of the vegetable matter of which it is composed*.

A few experiments were performed in the laboratory to test the maximum of temperature which the planktonic fauna could support. When a vessel of water was heated as gradually as possible from 35° to 45° C. (the whole process taking about half an hour), practically all the planktonic forms died suddenly when the temperature reached 42°–43° C. This experiment does not show that they would be able to survive for some hours at a point just below this temperature; nor, since the heating even in this experiment was rapid compared with that in Nature, that this was the absolute maximum of their endurance. On the other hand, the suddenness of their death at this point seemed to indicate that an important limit had been reached.

From the whole of these experiments and observations, it seems probable that the planktonic forms are often very close to their limit in temperature at midday, but that this limit is never exceeded. Except where they are forced to the surface by other conditions, there is always water of lower temperature available for them. There was no evidence from the behaviour of the fauna that it was controlled by variations of the temperature.

(6) *The Intensity of Ultra-violet Light.*—The evidence given in the previous pages indicates that it is improbable that the direct action of ultra-violet light had a dominant effect on the fauna, except occasionally in the clearest waters.

It is when the *respiratory exchanges* of the fauna are considered that the conditions of the habitat are found to be of a kind which must be of primary bionomic importance to the fauna. In particular, this is true of the supply of oxygen.

The average *oxygen-content* of the different waters during the summer months are given in the following table:—

	Day Maximum. c.c. per L.	Night Minimum. c.c. per L.	Average for 24 hours. c.c. per L.	Average for whole water. c.c. per L.
Shallow pool (C).				
Top	6.5	3	4.7	4.3
Bottom . .	6.0	2	4.0	
Deeper pool (D).				
Top	6.0	1	3.5	2.0
Bottom . .		Usually less than 0.5.		
Edge of swamp (A).				
Top		2–3 or less.		{ 1.5 (max.), often below 0.5.
Bottom . .		Usually less than 0.5 (often 0).		
Centre of swamp (B).				
Top		Less than 1.0 (usually .2–.3)		{ .50 (max.), usually 0.
Bottom . .		Always 0.		

* The eggs of some of the frogs also develop at the surface of the swamp (*Pseudicola* spp.).

These figures are necessarily rough, owing to the large variations in the amount of oxygen present at different times, but they give some idea of the relative amounts in the various waters. The parallel, which they show, to the results recorded in the table of the relative abundance of the fauna (p. 243) is striking.

The effects of different weather conditions upon the fauna gave further evidence of the importance of the supply of oxygen in controlling its life. Thus the unusual scantiness of the fauna of the outer part of the swamp in the latter part of November, when the oxygen-content was particularly low after a period of hot calm weather, was to be expected on this view. So also was the increase in the fauna of the central region of the swamp after the heavy rains of April, when more oxygen was found there. It is true that in some of the waters, where a shortage of oxygen is associated with poverty of the fauna, the water differed also in other ways from that in which more life was present. Thus, in the central part of the swamp there was a higher concentration of the chemical content of the water than elsewhere (alkali-reserve, phosphates, and carbon dioxide), and it is possible that these may have played a part in restricting the amount of life in the water. In this instance, where the chemical content was greater than anywhere else, the evidence for the predominant importance of the oxygen-supply is not conclusive. So far as the plants are concerned, it is very probable, the high chemical content was one reason for their absence. They would have been unaffected by the absence of oxygen, and, although the intensity of light in this water, heavily shaded by the overhanging vegetation, was very low, it might have been expected that some aquatic plant-life should have been found in it. It is clear that the animal plankton would have found a great obstacle to its survival in the low oxygen-content of the water, even if it had been able to live in water of this chemical constitution. It is certain that the chemical content dominated the life of the water nowhere except in the central region of the swamp. The pool C' was crowded with animal and plant life at many times, when the chemical content was as high as it ever was anywhere outside the central part of the swamp. Nor was there any correlation between the amount of life in the different waters and the concentration of the chemical content.

The shortage of oxygen in these waters raises the question of the minimum oxygen tension at which aquatic animals can survive. For fishes this is known to be surprisingly low. Pruthi (10) found that sticklebacks could live when the oxygen-content was as low as 0.25-0.5 c.c. per litre. For most fishes the limit is higher than this (1.7-0.4 c.c. per litre (Powers, 11)). In the swamps of the Chaco there is a large fish fauna. Many of the species are adapted to breathe air, but there are many others which do not do so. In view of the low oxygen tension at which fish are known to be able to live.

there is no discrepancy between the survival of the forms with aquatic respiration and the amounts of oxygen in these waters. In the central parts of the swamp, where the tension is almost always below the figures given by either of these authors, chiefly the air-breathing species are found. Elsewhere, when the tension falls too low (and it only occasionally falls below the figure given by Pruthi in all layers of the water in the outer part of the swamp), the species which do not breathe air satisfy their need for oxygen by making use of the thin surface layer of the water in contact with the air. This surface layer, which is probably much better aerated than the layers immediately below it, seems to be of great bionomic importance to many animals in these waters, the fish among them. Its importance will be discussed further in a later paper.

No data of the minimum oxygen need of the freshwater plankton are known to the authors. Some experiments to test this point for the smaller planktonic animals of these waters of the Chaco were performed, and will be more fully reported in a later paper. It may be stated here that the minimum was found to vary from 0.5-0.7 c.c. per litre for the amphipod (*Hyalella* sp.) to 0.2-0.3 c.c. for the smaller Crustacea and the rotifers. At these concentrations they were able to live for several hours, but it is not implied that they could do so indefinitely. At the times at which the water of the outer part of the swamp did not contain as much as 0.2 c.c. of oxygen in any of its layers, except presumably at the surface, the animal plankton began to die out. It has been stated above that the plankton was usually completely absent from the central part of the swamp where the oxygen-content was almost always below this figure during the hot weather. The survival of the amphipod, like that of the fish, is made possible by its habits. It is always to be found near the surface of the water among the weeds and waving its respiratory limbs in the surface layer.

The conclusion reached from all these observations is that the fauna of these waters shows by its behaviour that the need for oxygen is continually felt by it and that the supply of the gas is often dangerously low; but that there is no reason to think that its survival is inconsistent with the amount of dissolved oxygen which was found to be present in the water. An increase in the number of the animals would lead to a further fall in the oxygen tension and quickly bring it below the minimum for survival. On these grounds it seems probable that the oxygen tension is an important factor in controlling the life of the fauna.

No such parallel exists between the amount of *carbon dioxide* in the water and the quantity of life in it. Where over 100 c.c. of carbon dioxide per litre were present, truly aquatic life was usually scarce; but these waters were always rapidly drying up, and many factors were altering simultaneously in them. There was no evidence that it was the excessive carbon

dioxide that was especially the cause of the absence of life. It was probably one of several factors which together produced this result. Where the tension was that normal in these waters (50–80 c.c. per litre), no effects of its variation were to be observed in the behaviour of the fauna. In the pool C, where this amount of the gas was usually present, the most active and plentiful plankton found anywhere in the Chaco occurred in it.

The figure of 30 c.c. per litre of free carbon dioxide is given by Shelford and Allee as the limit of concentration which fish can endure in temperate waters. The estimates of the whole carbon dioxide-content, given in this paper, cannot be easily compared with this figure, but it seems certain that it was exceeded in the waters which gave the highest estimate (100–200 c.c. per litre). Even the foulest waters, which were generally those from which the highest estimate was derived, contained fish. It appeared that the fish in these swamps were not harmed by the highest carbon dioxide-content occurring in them. Their habit of using the surface layer for respiration may have made it possible for them to live in these waters. In the surface layer the water must contain not only more oxygen, but also less carbon dioxide.

It is therefore clear that the oxygen-content, alone of the series of non-biological characteristics of the environment which were investigated, undoubtedly plays an important part in controlling the life of the fauna during the hot weather. In exceptional circumstances it is possible that others, such as the intensity of the ultra-violet light and the temperature, may be important, but these circumstances are rare and their occurrence doubtful. It is very possible that there may be other factors outside the list of those which it was possible to study. Only a small number of the many which are simultaneously at play can be investigated at present, but it seems probable that none of those open to investigation are as important as the oxygen-supply in these waters.

The life of an animal in its environment is also dependent upon the biological conditions of the habitat. The most general relation of this kind is the dependence of the animal either directly or indirectly upon the flora for the provision of its food. In the swamps of the Chaco the phytoplankton was scarce. It is possible that this may have been of importance in limiting the increase of those animals whose food is the phytoplankton. The poverty of the zooplankton may have been partly due to this cause, but it would have had little effect upon other groups of animals which feed upon the aerial plants. The biological relations between the flora and fauna are outside the subject of the present paper.

The conditions which have been so far discussed have been those of the swamp-water during the hot weather, when the climate is tropical. The data given in the second section of the paper show that the climate has

considerable seasonal variation. This must be reflected in the conditions of its freshwater habitats, and the observations made in April and May show that this is so. At this time the conditions were greatly modified by the flooding which occurred then, but other changes were produced by the lower temperature (*e.g.*, the increased oxygen-content of the water). It was not possible to carry the investigation far enough into the cool weather to make a thorough study of the conditions at that time, nor for the object of the research, the study of the conditions in tropical freshwaters, was it of great importance to do so. It is of interest to note that the increase of oxygen in the water, especially in that of the central part of the swamp, was accompanied by an increase in the amount of the fauna.

The cause of the very low oxygen-content of these waters is undoubtedly complex. At least the following four factors must co-operate to produce it:—

(1) Only very occasionally, when the minimum air-temperature fell to 15° C. after a cool day, were the layers of the water mixed at night by convection currents due to the cooling of the surface. This has been discussed above.

(2) The water was protected from disturbance either by the floating blanket of weed or by the clumps of tall plants. Wherever the water was more open, much more oxygen was found in it. This was so in the small pools among the weed in the outer part of the swamp, which have been described above. It was also true of the rare pieces of open water which occurred in the country. Near the swamp were stretches of grassland which were frequently flooded in wet weather. In some of these, large excavations 3 or 4 feet deep had been made. These formed pieces of open water larger and deeper than the pools in the outer part of the swamp. The water was similar to the swamp-water in its more muddy parts, but a large amount of oxygen was present in it both in the surface layers and at the bottom (2–3 c.c. per litre). When the chemical content was not too great, which was only the case when the water was nearly evaporated, the plankton was plentiful.

(3) There was very little phytoplankton in any of the swamp-waters. Whatever the cause of this, it is clear that the absence of photosynthesis removed one source of oxygen. In the pools where the phytoplankton was plentiful the water often contained much oxygen.

(4) The large amount of decay in the water must have set up a heavy drain on any oxygen which reached it. The activity of decay is greater in the hot climate, and most of the oxygen in the water was probably used in this way.

It remains to consider how far the conclusion that the supply of oxygen for respiration is the factor of greatest bionomic importance among the

non-biological conditions of the environment is likely to be true for tropical waters elsewhere. Such a question can obviously only be approached with great caution in the present absence of evidence. In the central parts of lakes and other open pieces of water it is almost certain that this is not the condition of greatest survival value (at least in the upper layers of the water—*i.e.*, above the thermocline). There disturbance must be greater, the water purer, owing to the lower concentration of chemical substances brought from the land, and the decay taking place in the water much less. A very low oxygen-content is not to be expected in these waters. On the other hand, some of the factors which were found to produce the low oxygen-content of the waters of the Chaco will operate in all tropical waters. Thus the high temperature will prevent mixing of the layers of the water everywhere, and the activity of decay will be greater than in temperate countries. It would seem that waters in other parts of the tropics should show a similar shortage of free oxygen, if they are protected from the wind and if there is much decay taking place in them. Both these conditions will be produced if there is much growth of aerial plants above and on the surface of the waters. Only if the phytoplankton is plentiful in the water and photosynthesis active, will the shortage of oxygen be made up, and this will be largely prevented if the water is shaded by overhanging vegetation or is opaque.

Such waters must occur commonly in tropical countries. Many tropical swamps and the shallower parts of many lakes and slow rivers will be of this type. Probably most of the tropical waters which appear to have a rich supply of food-substances for the fauna and flora, but are poor in life, are so for this reason. Even in the open water of slow rivers, if there is no disturbance by the wind, it seems probable that the activity of decay in the water is sufficient to keep the oxygen-content low, so long as the growth of the phytoplankton is prevented either by the opacity of the water or its chemical constitution.

Two factors, both the result of the higher temperature, produce the differences between the conditions in these tropical waters and those in similar waters in the temperate zone. These are the absence of the mixing of the layers of the water at night and the greater activity of the processes of decay. In their absence the oxygen which is able to reach the water is more than sufficient for the decay which is going on in it, and a large fauna can live. Similar conditions to those in these swamps are found at the bottom of stagnant pools in temperate countries, where there is often very little oxygen and a very slight fauna; or in the hypolimnion of the larger lakes, where a lack of oxygen is again the cause of the scarcity of life. In other respects the nearest approach to the conditions of these waters is in the culture media of the laboratory; the large quantities of

phosphates, carbon dioxide, and probably of other chemical substances are similar.

The conclusion is therefore reached that the swamps of the Chaco, and probably many other shallow tropical waters, belong to the category of waters in which the condition of survival value to the greatest part of the fauna is the supply of oxygen for its respiratory needs. To the same category the hypolimnion belongs. If a term to describe the waters of this type is required, it may be suggested that "aerocratistic" is used. In distinction, waters in which the supply of the inorganic food-substances is the condition of greatest importance would be called "brotocratistic," and "chemicratistic" and "rheocratistic" would be used for the waters in which the chemical content and the current is of primary importance. Recent research has shown that the sea is a typically brotocratistic environment. Naturally saline waters are clearly chemicratistic.

APPENDIX I.

Geological Analyses of some Samples of Soil from the Paraguayan Chaco.

By B. H. BARRETT, M.A., B.Sc.

Four samples have been examined mechanically and mineralogically. They occur in the following stratigraphical order and at the depths shown:—

1. Depth 1–3 ft.
2. Depth 3–10 ft.
3. Depth 10–12 ft.
4. Depth greater than 12 ft.

The mechanical analysis was carried out by elutriation, and the results are shown on the graph (Pl. 13), in which the percentages are cumulative. The table shows the percentage of each grade.

	1.	2.	3.	4.
Greater than 0.25 mm. diam.	0.2	0.9	0.3	0.5
" " 0.1 mm. diam. and less than 0.25 mm. . . .	0.3	0.2	0.1	1.0
" " 0.05 mm. diam. and less than 0.1 mm. . . .	19.5	18.7	34.0	35.3
" " 0.01 mm. diam. and less than 0.05 mm. . . .	41.0	25.5	50.8	49.5
Less than 0.01 diam.	39.0	54.7	14.8	13.7

The strict geological explanation of these diameters is that material measuring between 1.0 mm. and 0.1 mm. is sand, between 0.1 mm. and 0.01 mm. is silt, and below 0.01 mm. is clay. In the samples no particles exceeded 1.0 mm. in diameter. Applying the terms sand, silt, and clay with these meanings, it is seen that the highest percentages of sand are in numbers 2 and 4. The specimens are best described as silts. Of this grade they contain about 60, 44, 85, and 85 per cent. respectively. The analyses

suggest that there is no essential difference between the samples which lie between 10 ft. and 12 ft., and those at a greater depth. Sample 2 shows the highest percentage of clay.

Bromoform separations were carried out on each sample, and although weighed quantities were used in each case, the amount of heavy residue was so small as to prevent accurate weighing with the facilities available. The minerals of both heavy and light residues varied greatly in size, but the majority were fairly angular in shape, especially in the light residues. In the latter the minerals were quartz, and the feldspars microcline, orthoclase, and albite. Those of the heavy residues were an interesting suite. The table shows the greatest number found in any residue, namely number 4, and variations from this will be noted for the other samples.

<i>Cubic.</i>	<i>Tetragonal.</i>	<i>Hexagonal.</i>	<i>Orthorhombic.</i>
Magnetite.	Zircon.	Apatite.	Hypersthene.
Garnet.	Rutile.	Tourmaline.	? Staurolite.
	Anatase.	Ilmenite.	? Topaz.
		Quartz.	
		Hæmatite.	
	<i>Monoclinic.</i>		<i>Triclinic.</i>
	Biotite.		Microcline.
	Chlorite.		
	Epidote.		
	Hornblende.		
	Muscovite.		
	Augite.		
	Monazite.		
	Orthoclase.		

Among the zircons there are two types: those which show perfect crystallographic outline and are small in size, and those larger ones which are rounded. A few are of the purple type that originally appear in pre-Palæozoic rocks. Garnet occurs as pink and colourless grains.

Both red and yellow shades of rutile are present, varying in shape from prisms to angular fragments.

Tourmaline, both blue and pinkish-brown, shows its crystal form only in the small specimens. The amount of this mineral is subject to variation in the samples from the different levels, as will be noted later.

The hornblende is always in long narrow fragments, and is pleochroic in shades of brown and green. In the residue of sample number 3 the mineral follows the iron for frequency.

The biotite, if that identification is correct, is interesting because of the excellent biaxial figure.

When they occur, monazite, epidote, apatite, and anatase are small in size and in quantity.

A mineral, of which no identification is offered, is present in all residues. It shows colourless prisms having a refractive index similar to that of apatite. Under crossed nicols the mineral shows a series of colour bands parallel to the *c*-axis, apparently due to thickness; they correspond with partings. It gives straight extinction, and the two vibration directions available in the specimens both have a refractive index above that of Canada Balsam. No basal sections have been observed; the nature of the interference figure is unknown. It appears, however, to be a positive mineral and may be topaz.

In all the magnetic residues there is much iron. The light residues are all stained with hæmatite. The light residues are seen to be highly angular, and the majority of the grains are of quartz. Among the feldspars, microcline and orthoclase have been identified. As is to be expected in deposits having the mechanical composition of these, the grains vary greatly in size.

An interesting relationship is seen in the residues from the four levels. Specimens 1 and 4 have the same mineral assemblage, but in 2 and 3 the assemblage is much reduced mainly by the reduction in the amount of tourmaline, garnet, epidote, and monazite in the magnetic portion. The greatest reduction is seen in the case of 3, in which the non-magnetic residue consists of zircon, rutile, and a little apatite only, and the magnetic of iron ores, hornblende, and a very small number of garnet and tourmaline grains. There appears, then, to be a progressive decrease in the assemblage from 1 down to 3, and then a sudden return to the maximum in 4.

This association of minerals appears to have been derived partly from acid igneous rocks and gneisses, while the large proportion of hornblende may have come from lavas.

APPENDIX II.

Chemical Analyses of some Samples of Waters from the Paraguayan Chaco.

By A. M'MILLAN, M.A., D.Sc., and other workers of the Chemical Department of Glasgow University.

The following analyses were carried on samples of water brought home in stoppered bottles from the Chaco. The samples were mostly of 250 c.c.; a few were of 500 c.c. The latter are marked * in the table.

Qualitative analyses of the inorganic ions were also carried out. In all the samples Na was present in sufficient quantity for recognition, and frequently K, Ca, and Mg. Traces of Fe were found in some of the samples, especially in those of water from flooded land.

Only one sample, that of a sample of saline water from pools in the bed of a stream, contained sufficient salts for quantitative analysis. The results of this analysis are given on opposite page.

	Depth.	Density at room temp.	Electr. conductivity.	Total residue.	Non-volatile residue.
	in.	gms. per 100 c.c.	$\times 10^4$.	gms. per 100 c.c.	gms. per 100 c.c.
I. Swamp-water.					
(1) Position A. (Outer part of the swamp.)					
1. 1.10.26. Just after light rain	6	1.000	3.319	.0284	.0166
2. 27.11.26. Just after light rain	4	1.000	..	.0324	.0145
3. 13.12.26 10 days after heavy rain	12	1.000	2.720	.0210	.0136
*4. 22.2.27 Rapidly drying	5	1.003	3.339	.0324	.0128
5. 9.4.27. Nearly dry	1.000?	5.670	.0369	.0162
*6. 6.6.27. Flooded	26	1.001	2.185	.0222	.0149
(2) Position B. (Centre of swamp)					
1. 13.12.26	1.001	4.070	.0281	.0125
2. 9.4.27. Nearly dry	1.000	4.507	.0340	.0082
3. 6.6.27. Flooded	1.000	3.210	.0310	.0147
(3) Centre of swamp. (Another position.)					
1. 6.6.27. Flooded	1.000	5.686	.0356	.0176
(4) Large piece of open water, 5 miles E. of Makthlawaiya.					
1. 4.2.27.	1.000	4.476	.0311	.0162
II. Water on flooded land.					
1. 27.12.26. Near swamp	1.000	2.150	.0225	.0120
2. 9.2.27.	1.001	2.339	.0380	.0222
3. 26.2.27. 5 miles S. of Makthlawaiya	1.000	1.406	.0124	.0046
*4. 13.5.27. Flood - water entering swamp	1.001	1.820	.0206	.0096
5. 8.6.27. Flood - water entering swamp	1.000	1.830	.0241	.0089
III. Rain-water pools.					
(1) Shallow pool, C.					
1. 22.2.27. Nearly dry	1.000	1.950	.0229	.0105
*2. 21.4.27. After rain. Full999	.7251	.0166	.0026
(2) Deeper pool, D.					
1. 22.2.27. Nearly dry	1.001	3.650	.0346	.0156
*2. 21.4.27. After rain. Full	1.000	2.277	.0583	.0234
(3) Other pool in pasture.					
1. 9.2.27	1.001	2.339	.0380	.0222
IV. Waters of the streams.					
1. 16.10.26. Drying pools	1.015	244.4	1.986	1.986
2. 18.12.26. After rain.	1.003	59.0	.3643	.2067
3. 19.5.27. Flooded	1.001	20.72	.1237	.0748
V. Water of well in silt.					
1. 1.10.26. Makthlawaiya	1.001	11.42	.0648	.0548

Quantitative analysis of the water of the saline pool of density 1.015 (IV. 1) :

Na	0.5900	gms. per 100 c.c.
K	0.0667	" "
Ca	0.0508	" "
Mg	0.0421	" "
Fe	Trace.	
Cl	0.7938	" "
So ₄	0.4070	" "

SUMMARY.

(1) A general description of the Paraguayan Chaco and its swamps is given. These swamps belong to the type of tropical waters which have an abundant food-supply and a comparatively poor fauna and flora of truly aquatic forms.

(2) An investigation of the waters of these swamps was carried out with the object of determining the relative importance of various conditions of the environment to the life of the aquatic fauna.

(3) The conditions chosen for investigation were :—

1. Temperature.
2. Hydrogen-ion-concentration.
3. Alkali-reserve.
4. Carbon dioxide-content.
5. Oxygen-content.
6. Phosphate-content.
7. Penetration of ultra-violet light.

(4) In the hot weather the distribution of the fauna was chiefly controlled by the oxygen-content of the water. This was very low in the water of the swamp.

(5) The variations of the other conditions, except occasionally of the ultra-violet light and the temperature, are not of great importance to the fauna.

(6) In the production of this low oxygen-content at least the following conditions co-operate :—

1. Temperate changes at night did not cause mixing of the layers of the water. This was a result of the hot climate.
2. The water is protected from disturbance by the presence of much vegetation above it.
3. The opacity of the water, and probably other causes, prevented the growth of a large phytoplankton.
4. There is a large amount of bacterial decay in and above the mud at the bottom of the water.

(7) During the hot weather the changes which followed rain were the most important to the fauna of those produced by conditions external to the water. This is usual in tropical waters. It was not possible to carry the investigation through the cooler weather.

(8) In certain rain-water pools, which were investigated for comparison with the swamps, a more abundant phytoplankton and more oxygen in the water were associated with much more animal life.

(9) It is suggested that similar conditions will be found to occur in other tropical waters which resemble those of these swamps in the following respects:—

1. A small phytoplankton either on account of the opacity of the water or its unsuitable chemical composition.
2. The absence of disturbance.
3. The presence of much aerial plant-life in and around the water.

Most tropical swamps and the shallower and quieter parts of many large rivers and lakes probably belong to this category.

Further evidence of the importance of the supply of oxygen to the fauna of these swamps will be given in later papers in a description of its adaptations to meet this need.

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EXPLANATION OF THE PLATES.

PLATE 9.

- Fig. 1. A view over the swamp from its edge. In front the outer region, filled with sedges in the foreground and covered with floating weed in the middle distance. In the background, clumps of *Thalia*.
- Fig. 2. A nearer view of the edge of the central part of the swamp at a place where the clumps of *Thalia* are thick. Foreground: water up to 1 foot deep, filled with sedge and grass. The scale of the clumps of the tall plants is given by the cow.
- Fig. 3. A position similar to that described as A. Foreground and middle distance: water 1-2 feet deep, with sedge and floating weed. In the background, open pools and clumps of *Thalia*.
- Fig. 4. A small, open pool among the clumps of *Thalia*. Foreground: water 3 feet deep, covered with *Pontederia*. The position described as B was at a position similar to this, but among the stems of the tall clumps of *Thalia*.

PLATE 10.

- Fig. 5. The central part of the swamp in a part where it is filled with bulrushes (*Typha* sp.).
- Fig. 6. A near view of the floating blanket of vegetation in the outer part of the swamp. The larger plant is *Pistia*, the smaller the water-ferns *Salvinia* and *Azolla*.
- Fig. 7. The deeper pool (D).
- Fig. 8. The shallower pool (C).

PLATES 11 & 12.

Observations taken in the outer part of the swamp.

PLATE 13.

Analyses of soil-samples from the Chaco.



SWAMPS OF THE

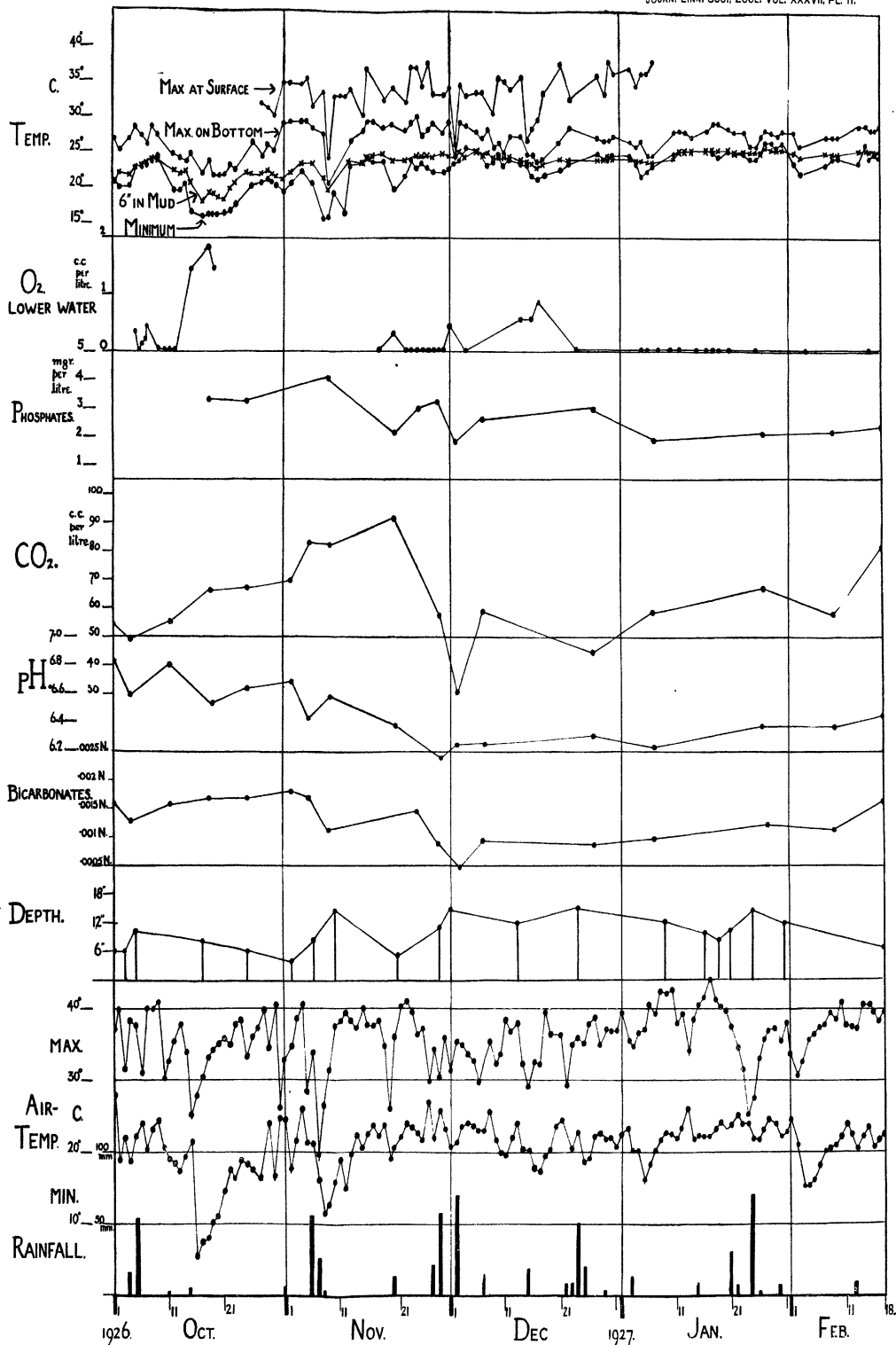


PARAGUAYAN CHACO.

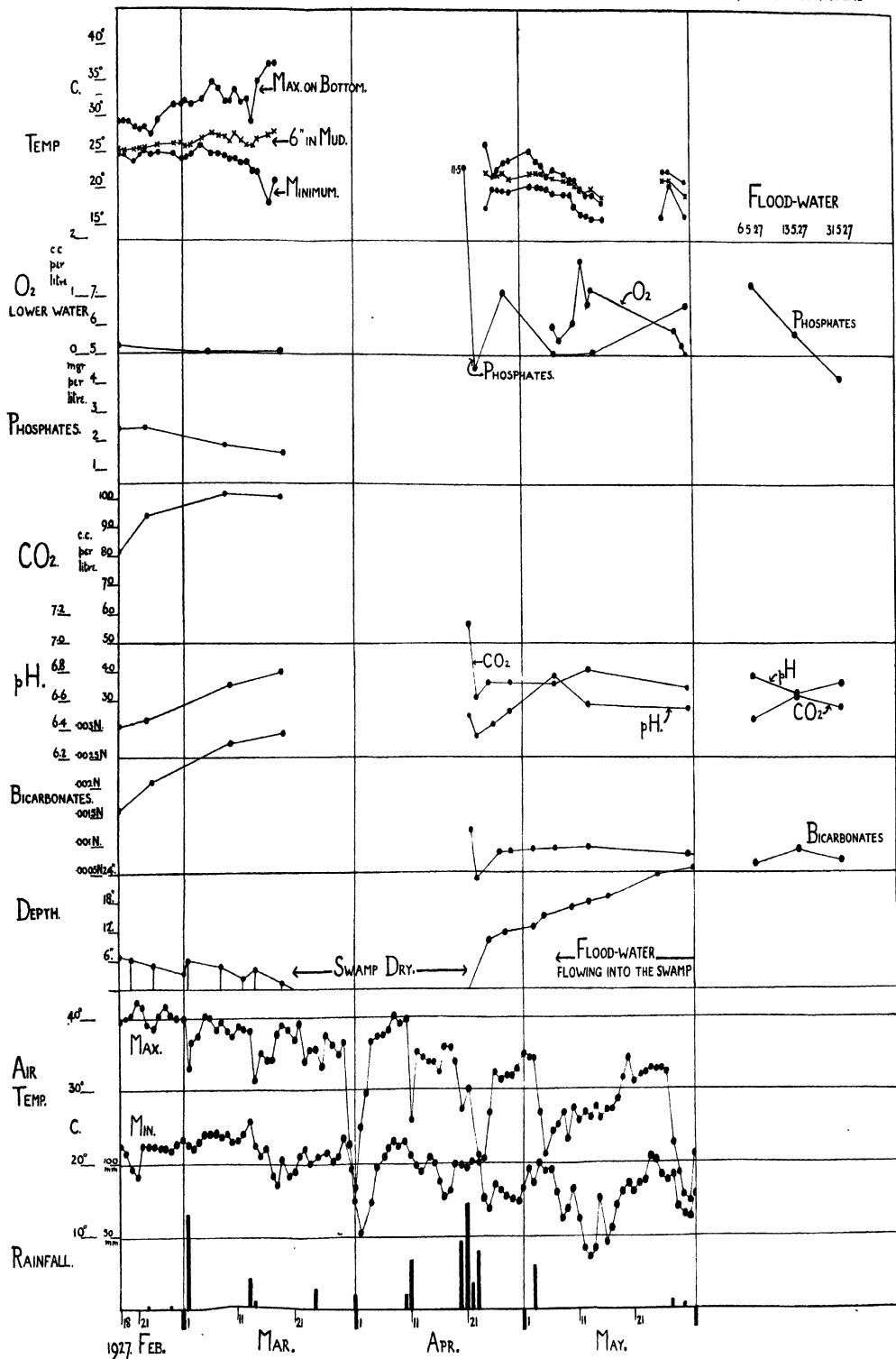




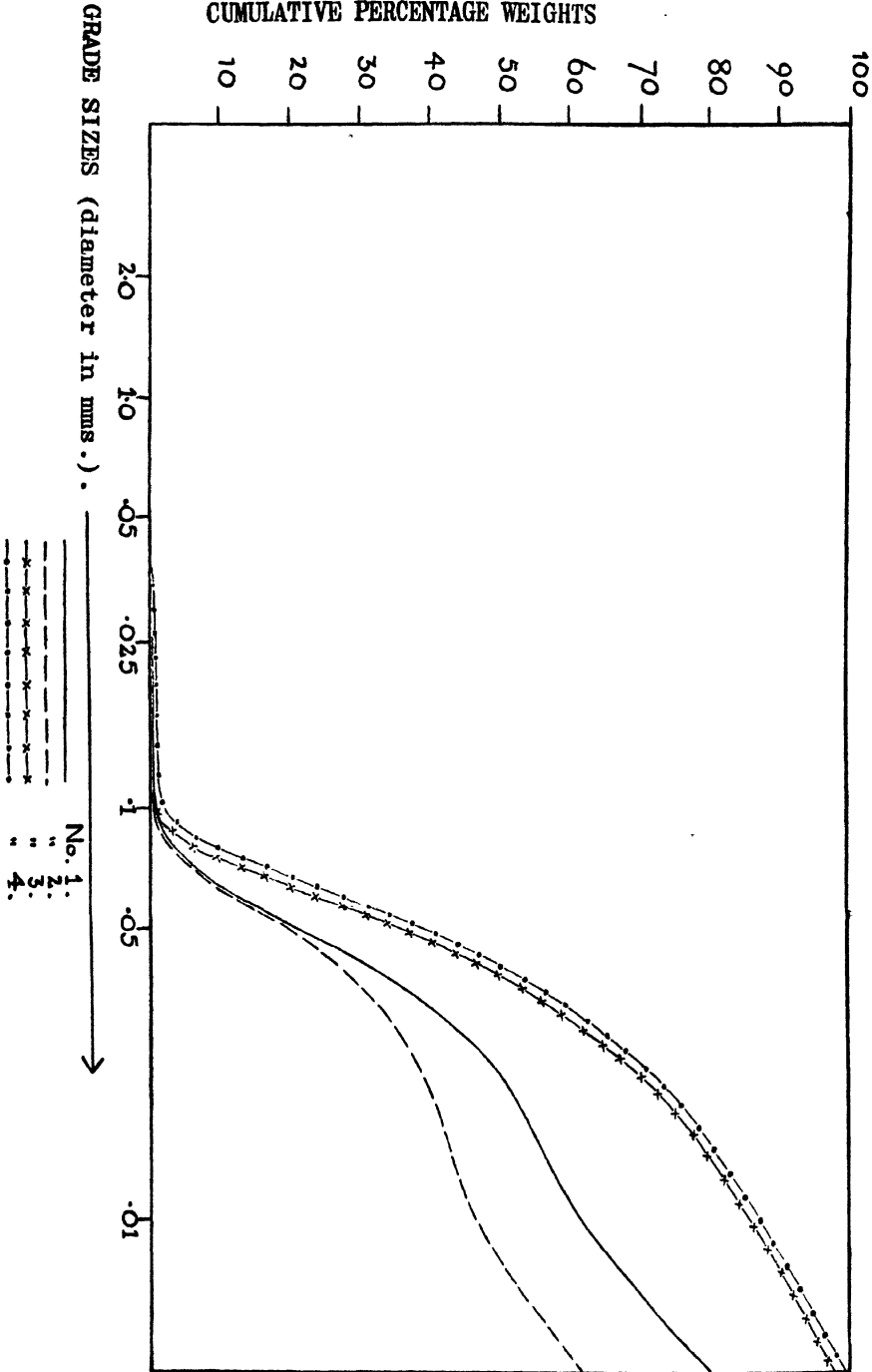
PARAGUAYAN CHACO.



Physico-chemical observations in the Swamps of the Paraguayan Chaco.



Physico-chemical observations in the Swamps of the Paraguayan Chaco.



Geological analyses of some samples of soil from the Paraguayan Chaco.

Reports of an Expedition to Brazil and Paraguay in 1926-27, supported by the Trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for Scotland.

Argulidæ. By WILLIAM A. CUNNINGTON, M.A., D.Sc., Ph.D., F.L.S.

(PLATES 14 & 15.)

[Read 3rd January, 1929.]

1. INTRODUCTION.

The material collected by Dr. G. S. Carter during his South American expedition contained a few specimens of Argulidæ, which he has kindly placed in my hands for examination and report. It is not very often that South American Argulids reach this country, and I was the more interested in this small collection since I have for some time been engaged in studying the members of the almost exclusively South American genus *Dolops*.

Although consisting of but twenty-four specimens, the present collection is quite an interesting one, containing representatives of three species belonging to two genera—two species of *Dolops* already known from this region, and a species of *Argulus* which appears to be new to science. The following is a list of the species obtained:—

Dolops striata (Bouvier).

„ *geayi* (Bouvier).

Argulus carteri, sp. n.

All the specimens were obtained from the same host-fish—the Characid *Hoplias malabaricus* (Bloch)—and from the same locality, Makthlawaiya, in the Paraguayan Chaco, the position of which is approximately 58° 19' W. by 23° 25' S.

By the courtesy of the authorities of the Paris and Berlin Museums certain species of *Dolops* were lent to me for purposes of comparison. These enabled me to confirm my provisional determination of these forms; I would here express my indebtedness to Professors Gravier and Schellenberg for the trouble they have taken in the matter.

For the purposes of illustration I have * again had recourse to low-power photography on a black background, which conveys all that can be expected of a general figure. I have to thank Professors Huxley and Mackinnon for permission to use the photographic apparatus in the Zoological Department of King's College, London.

* Cf. Proc. Zool. Soc. 1913, pls. xli and xlii.

2. SYSTEMATIC NOTES AND DESCRIPTION OF NEW SPECIES.

Family ARGULIDÆ.

DOLOPS STRIATA (Bouvier). (Pl. 14. figs 1-4.)

Gyropeltis striata Bouvier, Bull. Mus. d'Hist. Nat. Paris, tome v, 1899, p. 40.

Dolops striata Bouvier, Bull. Soc. Philom. Paris, sér. 8, tome x, 1898 (1899), p. 77.

Dolops striata Wilson, Proc. U.S. Nat. Mus. vol. xxv, 1903, p. 735.

Dolops striata Thiele, Mitt. Zool. Mus. Berlin, Bd. ii, Heft 4, 1904, p. 10.

This species was originally described by Bouvier from two female specimens collected by M. Geay in Guiana, on the Franco-Brazilian border. The description given was quite sufficient to enable the species to be recognized, and male specimens have since been described by Thiele. The host of the type-specimens is given merely as "une Anguille"*. According to Thiele the species was obtained by von Jhering on various freshwater fishes in the neighbourhood of Porto Alegre†.

The specimens obtained by Dr. Carter are as follows :—

No. 1183, 22/4/27 ... 5 males and 6 females.

No. 1273, 12/5/27 ... 1 female.

These all came from the same host—*Hoplia smalabaricus* (Bloch)—and from the same locality, Makthlawaiya. This is the first definite record of a host for this species.

The dimensions of the largest specimen (an ovigerous female), which is considerably larger than either of those examined by Bouvier, are worth putting on record :—

	mm.
Total length	13·0
Length of carapace.....	10·2
Breadth of carapace	11·2

While the descriptions and figures of Bouvier and Thiele suffice for identification, I add here figures to illustrate the general form and markings (Pl. 14. figs. 1-4). Those of the female are taken from the largest specimen in this collection, those of the male (for sake of comparison) from a large individual in the collection of the Berlin Museum.

* I am informed by Mr. J. R. Norman, of the British Museum, to whom I am indebted for the correct name of the host-fish, that there are no freshwater eels known from South America. He suggests that the "eel" here mentioned was probably a species of *Symbranchus*.

† There is more than one place of this name shown on the map of Brazil. The Porto Alegre referred to is probably that in the province of Rio Grande do Sul, some 150 miles north of the town of that name.

DOLOPS GEAYI (Bouvier). (Pl. 14. figs. 5-7.)*Gyropeltis geayi* Bouvier, Bull. Mus. d'Hist. Nat. Paris, tome iii, 1897, p. 13.*Dolops geayi* Bouvier, Bull. Soc. Philom. Paris, sér. 9, tome i, 1899, p. 17.*Dolops geayi* Wilson, Proc. U.S. Nat. Mus. vol. xxv, 1903, p. 736.

Like the preceding species this was described by Bouvier from specimens collected by M. Geay. The collection, which came from Venezuela, merely consisted of two males and one small (probably immature) female. No host was known, as the specimens were obtained free from the surface of lagoons.

One of the original examples studied by Bouvier was kindly lent to me for examination, and when, a little later, further *Dolops* material reached me from Berlin, I was gratified to find among certain unidentified specimens seven individuals belonging unmistakably to this species. Mature forms of both sexes were represented, these being considerably larger than those originally obtained. When Dr. Carter's collection came into my hands still more recently, I was interested to discover that nearly half the specimens belonged to this species, and that, in point of size, some of them were yet larger than those from Berlin. As the material now available for study is so much more extensive, a revised specific description is called for. This description, and the accompanying figures, I hold over, with the approval of Dr. Carter, for publication in a paper dealing with the genus *Dolops*, which is in course of preparation. Photographs to illustrate general form and pigmentation etc. are, however, included here (see Pl. 14. figs. 5-7).

The following is a list of the specimens in this collection:—

No. 1183, 22/4/27 3 females.

No. 1232, 3/5/27 1 male.

No. 1246, 9/5/27 2 males.

No. 1273, 12/5/27 ... 1 male and 4 females.

They were obtained at Makthlawaiya on *Hoplias malabaricus* (Bloch). This constitutes also the only definite record of a host for this species.

ARGULUS CARTERI, sp. n. (Pl. 14. figs. 8-9 ; Pl. 15. figs. 10-14.)

Description.—Carapace (in the female) elliptical, considerably longer than broad, with slight antero-lateral depressions. Posterior lobes moderately broad and rounded, covering bases of first and second swimming-legs and nearly covering third swimming-legs in ovigerous female. The lobes are separated by a moderately broad sinus about one-third the length of the carapace. The edge of the carapace below is well armed with small spines, which extend into the region of the swimming-legs. Abdomen in the female slightly longer than broad, about one-fifth entire length of body ; posterior lobes somewhat pointed, but with rounded tips, and separated by broad sinus two-fifths length of abdomen. The furcal appendages are borne on the margins of the anal sinus one-fifth of its length from the bottom. Antennules

and antennæ large and well armed, approaching somewhat to one another in the mid-line. Basal segment of the antennule with stout posterior spine; second segment with anterior hook, posterior spine, and well-developed lateral hook. Antennæ with stout spine on basal segment. Immediately behind the insertion of the antennule is situated a stout accessory spine. Eyes rather large, less than one-fifth breadth of carapace apart. Suckers rather large, $\cdot 15^*$ of breadth of carapace. Maxillipeds moderately strong and well armed; basal segment produced into three stout spines; "area" rather small, oval, and only poorly armed. A pair of stout accessory spines is situated between the bases of the maxillipeds, and a second pair a short distance behind them but somewhat further apart. Flagella present on the first two pairs of swimming-legs. In the female basal segment of fourth leg produced postero-laterally into pointed lobe. Colour (in spirit) light yellowish brown with conspicuous markings of dark brown on carapace, thorax, and abdomen.

Dimensions as follows :—

Adult female (only specimen).	
	mm.
Total length	4.0
Length of carapace	2.8
Breadth of carapace	2.1

Remarks.—It is unfortunate that this species has to be described from a single specimen. The latter is, however, an ovigerous female, and it exhibits such distinctive features that I have no hesitation in regarding it as new to science. The dorsal markings are quite striking, and presumably characteristic. Furthermore, the somewhat uncommon position of the furcal appendages distinguishes the species, so far as I am aware, from any of the other South American forms.

Since the shape of the basal segment of the fourth leg (as seen from below) is subject to considerable variation within the limits of the genus, I include a figure illustrating its exact form in this species (Pl. 15. fig. 13). Again, as the supporting rods or rays of the sucker-margin ("Chitinspangen" of Thiele, "Chitin ribs" of Wilson's later works) differ greatly in different species, and have been repeatedly figured in recent papers, I have illustrated the condition in *A. carteri* (Pl. 15. fig. 14). While the features mentioned in the specific description must be regarded as those of primary systematic importance, the apparently meaningless variations of these chitin rays afford additional evidence which it would be unwise to ignore.

I have made an attempt to find the approximate position of this species in the only published key to the genus, namely, that given by Wilson in his review of the Argulidæ. It comes under the headings A'', in which carapace-

* Diameter of sucker measured at chitinous supporting ring, and not at extreme edge.

lobes do not reach abdomen ; B, in which anterior swimming-legs have full-sized flagella ; and C', in which the carapace is elliptical and considerably longer than wide. It will not, however, fit into either D or D' (the two subdivisions of C'), but merits a new subdivision in this part of the key. The number of described species of *Argulus* has increased very greatly since 1902 ; but in a relatively recent paper Wilson states that he has incorporated the newer forms in a manuscript edition of his key. It would be a matter of satisfaction if this could be made available for other workers on this group.

Occurrence.—Collected at Makthlawaiya, Paraguayan Chaco, on the Characid fish *Hoplias malabaricus* (Bloch). Reference No. 1192, 24/4/27.

3. GENERAL REMARKS.

This collection has added not inconsiderably to our knowledge of the South American Argulidæ. An addition has been made to the number of South American species of the genus *Argulus*, while the *Dolops* material has afforded further information of systematic value.

It is interesting to compare the distribution of these two genera as far as South America is concerned. The genus *Dolops* would appear to be represented by a larger number of species, though there is no great disparity. Including the form here described for the first time, the South American representatives of the genus *Argulus* now number six. The corresponding number of species of *Dolops* so far recorded is seven. An examination of the literature of the subject seems also to suggest that *Dolops* is more frequently obtained in this region than *Argulus*, and the collections in the British Museum confirm this view.

There can be little doubt as to the correctness of the opinion generally held that *Dolops*—in which hooks are never replaced by suckers—is the more primitive of these two genera, and in this connection attention may be drawn to the suggestion made by Thiele, namely, that tropical South America ought perhaps to be looked upon as the centre of origin of the Argulidæ as a whole.

The host-records given in this paper are a matter of some interest, since no precise records for these forms were in existence. It is rather striking that the three species in the collection—two of *Dolops* and one of *Argulus*—should all have been taken from the same species of fish. At the same time, the association of host and parasite among the Argulidæ is by no means so definite and consistent as it is in the case of other parasitic groups.

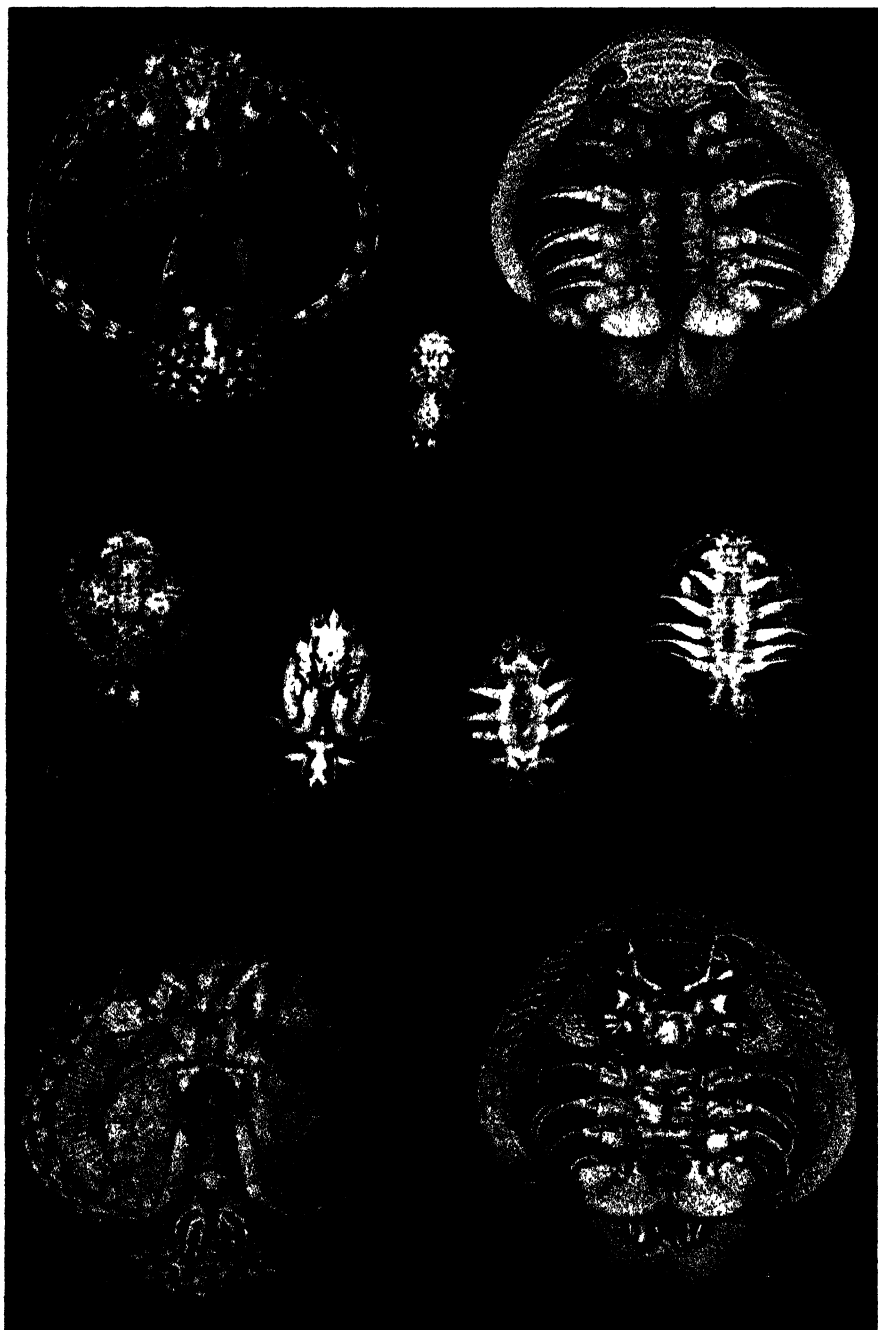
EXPLANATION OF THE PLATES.

PLATE 14.

- Fig. 1. *Dolops striata* (p. 260). Female, dorsal view. $\times 4\frac{1}{2}$.
 2. " " Female, ventral view. $\times 4\frac{1}{2}$.
 3. " " Male, dorsal view. $\times 4\frac{1}{2}$.
 4. " " Male, ventral view. $\times 4\frac{1}{2}$.
 5. *Dolops grayi* (p. 261). Female, dorsal view. $\times 5\frac{1}{2}$.
 6. " " Female, ventral view. $\times 5\frac{1}{2}$.
 7. " " Male, dorsal view. $\times 5\frac{1}{2}$.
 8. *Argulus carteri* (p. 261). Female, dorsal view. $\times 7$.
 9. " " Female, ventral view. $\times 7$.

PLATE 15.

- Fig. 10. *Argulus carteri*. Antennule and antenna. $\times 60$.
 11. " " Maxilliped. $\times 60$.
 12. " " Abdomen, dorsal view. $\times 60$.
 13. " " Fourth swimming-leg, ventral view, to show form of basal segment. $\times 60$.
 14. " " Portion of sucker-margin. $\times 360$.

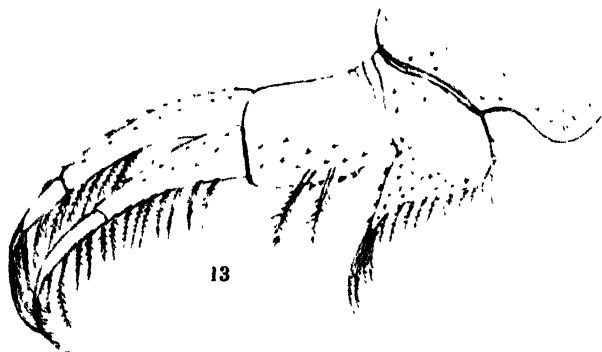
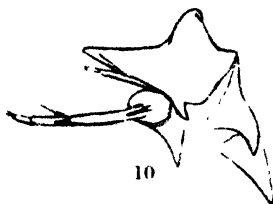
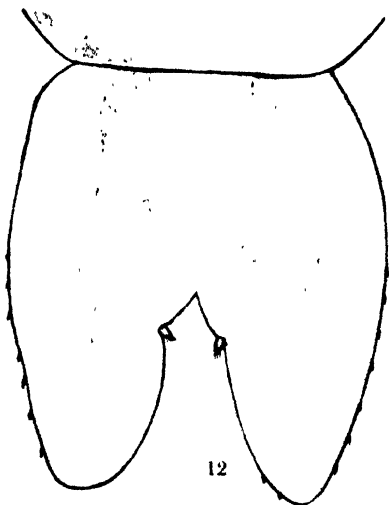
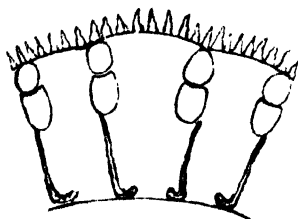
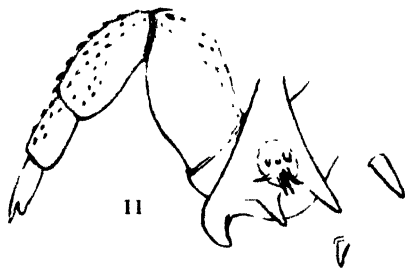


W.A.C. photo.

1-4 DOLOPS STRIATA.

5-7 DOLOPS GBAYI.

8, 9 ARGULUS CARTERI.



W.A.C. del.

ARGULUS CARTERI.

Reports of an Expedition to Brazil and Paraguay in 1926-7, supported by the Trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for Scotland.

Branchiopoda. By R. GURNEY, D.Sc., F.L.S.

(With 24 Text-figures *.)

[Read 3rd January, 1929.]

THE species of Branchiopoda here described were collected by Dr. G. S. Carter at Makthlawaiya (long. $58^{\circ} 19'$ W., lat. $23^{\circ} 25'$ S.) and Nanahua (long. $59^{\circ} 30'$ W., lat. $23^{\circ} 30'$ S.), and I am indebted to him for entrusting them to me for examination. The collection included five species, of which it is necessary to describe three as new. The other two species are *Leptestheria vanhoeffeni* Daday and *Cyclestheria hislopi* (Baird). As Dr. Carter has the intention of writing a full account of his work in this district, it is not necessary to describe the localities in detail.

DENDROCEPHALUS MIRUS, sp. n.

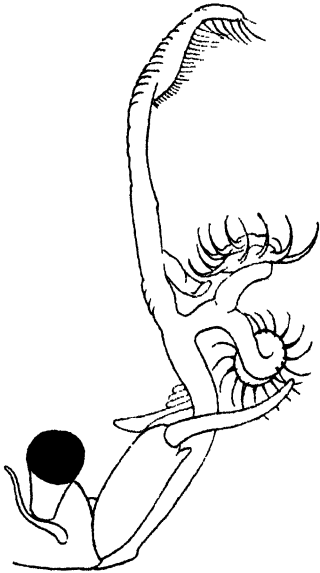
Male.—Frontal processes of extraordinary size, sometimes equal to half the length of the body. These processes are united at their base, and consist of a pair of long flexible appendages, from each of which springs a branch directed forwards and inwards. Each branch bifurcates, and each secondary branch is coiled into a close spiral, set along the margin of the coil with long curved spines. The two coils of one side are generally apposed to those of the other. From the main appendage, proximal to the branch, spring six narrow lappets on the ventral side. The proximal one of these is the longest, and is dilated and spoon-shaped at the end. The others decrease in size from behind forward. Distal to the branch is a broad flattened process turning upwards and inwards towards the body, with small spines along its edge. The appendage terminates in a flattened, very flexible portion, which is armed on both sides with many spines.

The second antenna is a simple two-jointed clasping appendage, the first joint having a small spine on its inner margin and a small finger-like process distally at the base of the long curved claw. Ventrally, in the middle line between the antennæ, is a pair of spines.

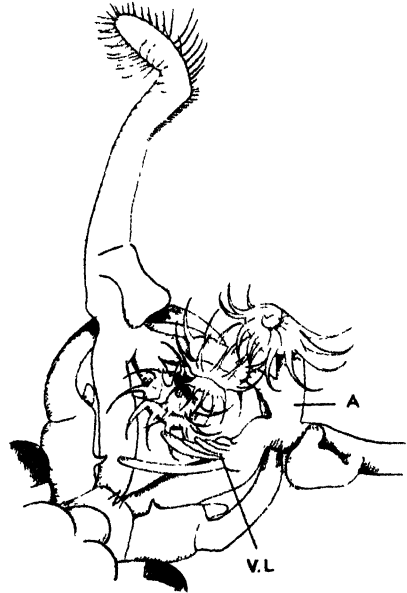
The everted penis is a large cylindrical organ armed with spines along each side.

* The cost of the text-figures has been met from the Westwood Fund.

TEXT-FIG. 1.



TEXT-FIG. 2.



TEXT-FIG. 3.

*Dendrocephalus mirus*, sp. n. Male.

Fig. 1.—Side view of head, showing the frontal process fully extended.

Fig. 2.—Ventral view of head, to show position and arrangement of the coiled inner branches. V.L., ventral lappets; these are omitted on the right side.

Fig. 3.—Part of main stem with ventral lappets, and branch A with coiled, spine-bearing, secondary branches, more enlarged.

The furcal rami are as long as the last four somites and fringed with long stout setæ, but without spines. The first two pairs of legs are of the same form as the succeeding pairs, the terminal endite not modified as it is in *D. geayi*.

Length 8–10 mm.

Female.—First antenna broad and rounded at the end. Egg-sac at base as broad as the abdomen, but constricted behind the second somite and tapering. It reaches to the seventh somite, or even to the base of the furca.

Length 8.5–12 mm.

From some coloured drawings made from the living animal by the collector it appears that there is some sexual difference in colour. In both sexes the furcal rami are brick-red, but while the body of the female is pale reddish brown, except where the intestine or the ovaries show through (the latter dark green), the male is pale blue except for the legs, which are faintly tinged with yellowish brown. This description of the colour applies to the appearance on a dark background.

TEXT-FIG. 4.



Dendrocephalus mirus. Everted penis.

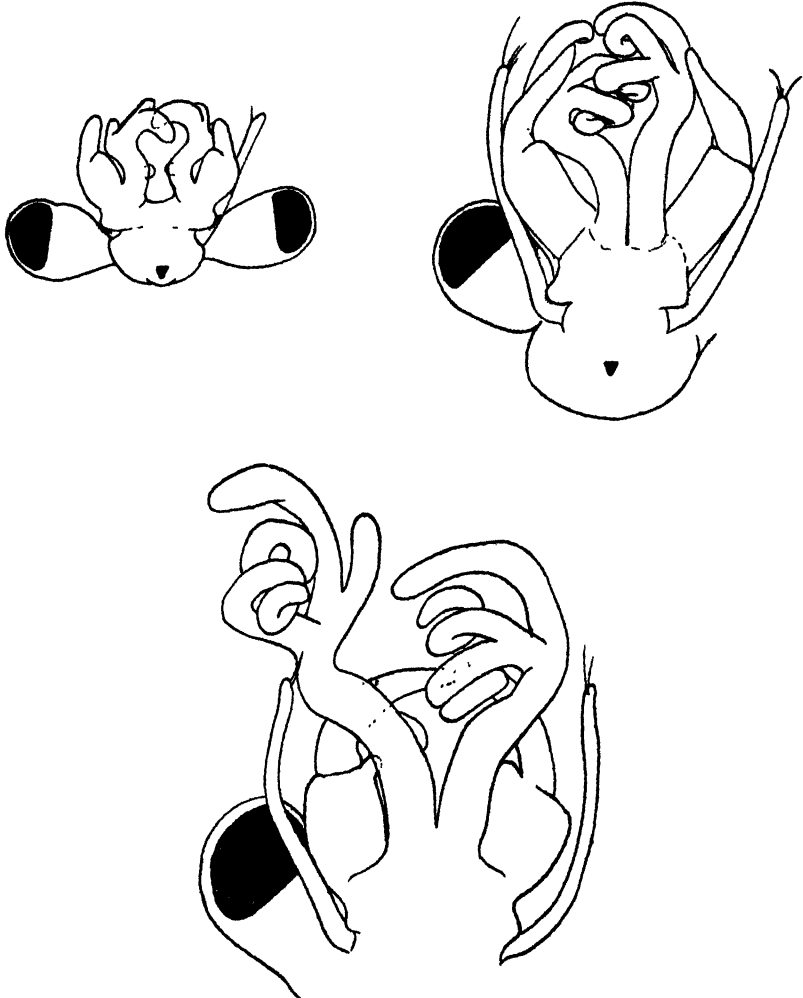
This species, while having the characters of the genus, differs greatly in the form of the frontal appendages from any of the three species hitherto described. In all these species these processes are united for a considerable distance, and the terminal part is branched in a complicated manner instead of being simple. The genus is confined to South America.

Occurrence.—Pools at Makthlawaiya and Nanahua ; common.

A particularly interesting feature of this remarkable species is the mode of development of the frontal processes. In young males in which all the legs are present and the rudiment of the penis is visible there is no median outgrowth, but there springs from the second antenna on its inner side a simple cylindrical outgrowth curving inwards and with three small branches. In the next stage these processes are larger, but they are still quite clearly outgrowths of the basal part of the second antenna. In an older specimen they have attained very much the adult form, the inner

branches being spirally coiled, but there are no spines. They are now, however, closely apposed at their base, and seem to spring from a common plate with the second antenna.

TEXT-FIGS. 5-7.



Dendrocephalus mirus, sp. n.

Figs. 5-7.—Three stages in the growth of the frontal organs of the male.

There is, then, no doubt that these processes are, in this species, outgrowths of the basal joint of the second antenna, even though in the adult they may be fused at the base and appear as a median outgrowth from the head*.

* Evans (Journ. Morphol. xxvi, 1915) came to the conclusion, on morphological grounds, that the frontal appendage of *Thamnocephalus*, which is a branched structure similar to that of *Dendrocephalus*, represents the inner branch of a bisamous second antenna.

Such large median outgrowths are frequently seen in the Anostraca, and are sometimes branched in a complicated manner, though rarely so much as in *Dendrocephalus*.

On the other hand, the genus *Chirocephalus* is characterized by having large and more or less complicated expansions of the second antenna.

It is probable that all these outgrowths, whether distinct from the second antenna in the adult or not, are homologous; but it is desirable that the development should be followed in other species. The term "frontal processes" is an unfortunate one, since it implies homology with the preoral frontal processes of Cirripedes and some larval Decapods, with which these organs have no relation.

TEXT-FIG. 8.

TEXT-FIG. 9.

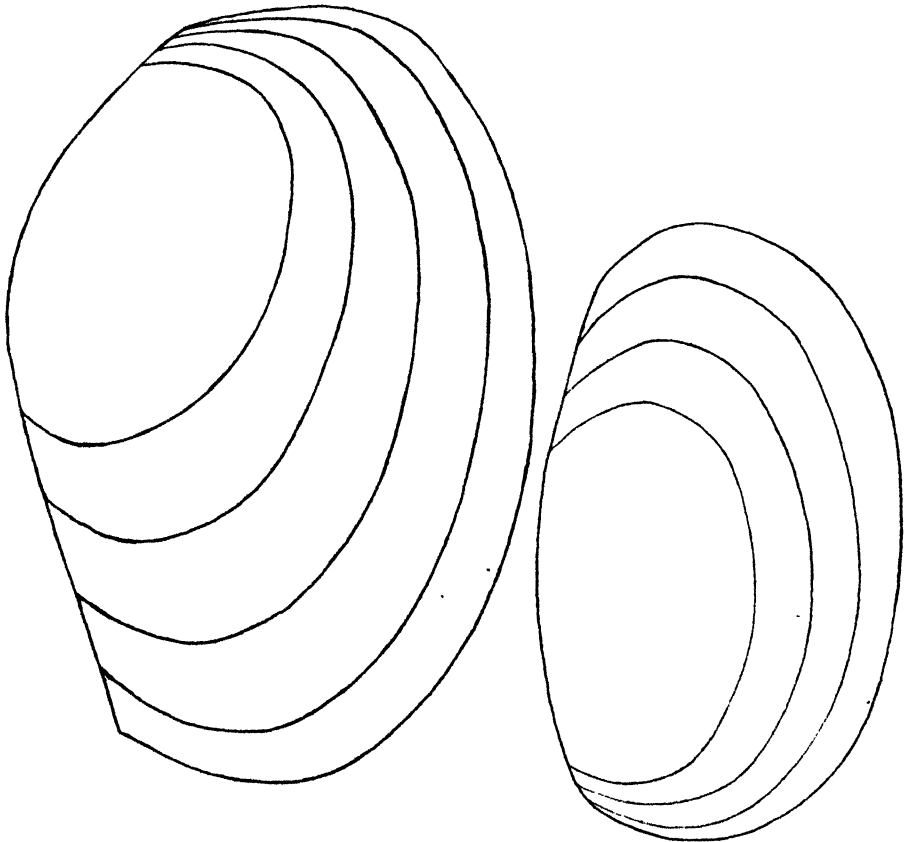
*Eulimnadia chacoensis*, sp. n.

Fig. 8.—Shell of female. Fig. 9.—Shell of male.

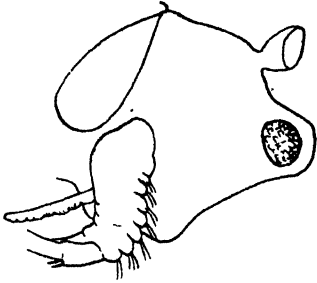
EULIMNADIA CHACOENSIS, sp. n.

Shell thin and transparent, with three or four very inconspicuous lines of growth and no definite markings. In the male the dorsal outline is gently

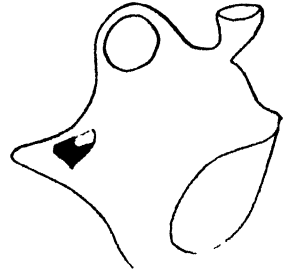
curved, with rounded anterior and posterior angles, while in the female it is rather more boldly arched dorsally, and there are distinct anterior and posterior angles.

	Female.	Male.
Length of shell	9.5 mm.	7.5 mm.
Greatest height	6.5 mm.	4.3 mm.

TEXT-FIG. 10.



TEXT-FIG. 11.



TEXT-FIGS. 12 & 13.



Eulimnadia chacoensis, sp. n.

Fig. 10.—Head of female.

Fig. 12.—Telson of female.

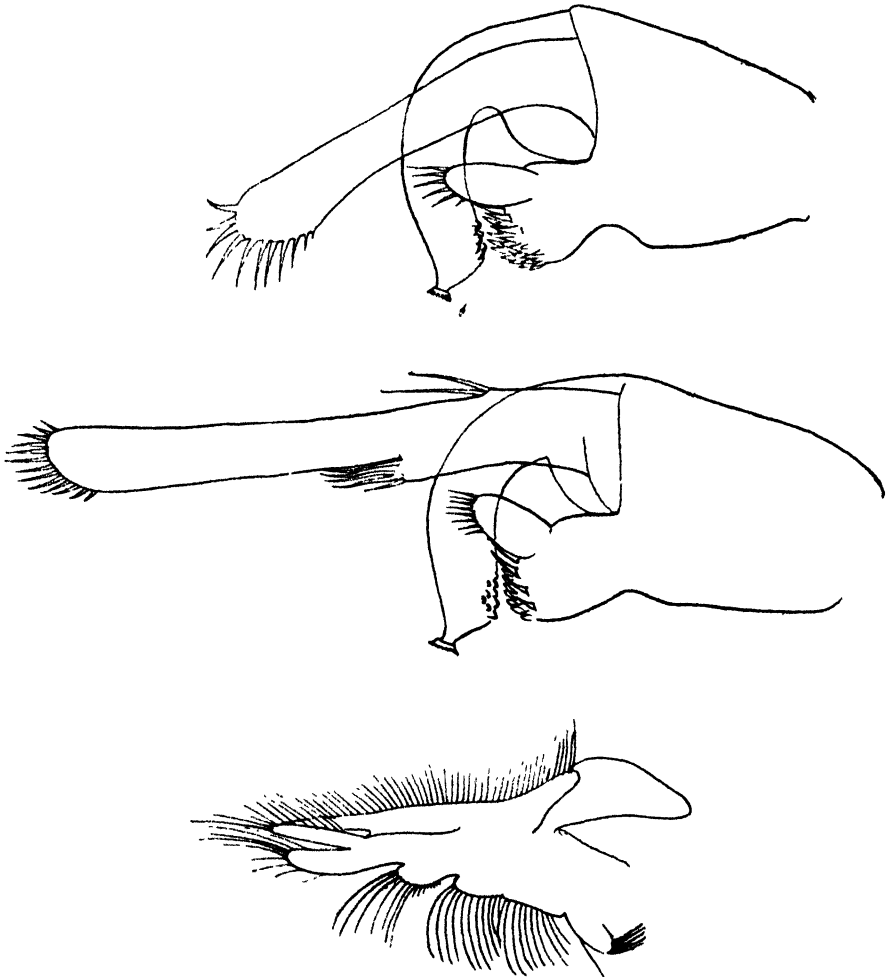
Fig. 11.—Head of male.

Fig. 13.—Telson of male.

Rostrum of female bluntly rounded, that of the male somewhat produced and pointed.

There are eighteen pairs of legs, and the posterior somites of the body are armed dorsally with small spines or short setæ. The number of somites

TEXT-FIGS. 14, 15, & 16.



Eulimnadia chacoensis, sp. n.

Fig. 14.—Part of leg 1 of male.

Fig. 15.—Part of leg 2 of female.

Fig. 16.—Leg 1 of female.

so armed varies from 7 to 10, and in one female examined they were arranged as follows, from behind forwards :—

0, 3, 4, 4, 4, 6, 4, 3, 3, 1.

The spines or setæ in each row are more or less of equal size, the middle ones not conspicuously larger than those on either side.

The telson in male and female nearly alike, except that the marginal spines are larger in the latter and the ventral prominences at the base of the claws are longer and more slender. The claws bear long setæ proximally for about two-thirds of their length. At about the second third there is a small spine, and beyond that point the claws bear very small spinules.

Leg 1 of the male with a very slight prominence distally on the inner margin of the clasper; leg 2 without any prominence or notch.

I am reluctant to describe this species as new, since the male differs scarcely at all except in size from *E. brasiliensis* Sars. On the other hand, the rostrum in the male is by no means so prominent as in that species, and the female differs not only in the form of the shell, but also in that of the rostrum, from Daday's description. There are also smaller differences in the telson, and particularly in the dorsal armature of the somites. These are shown by Daday as bearing long setæ in the female on the last three somites, whereas in my own specimens these somites bear only very small spines, and the last somite may be unarmed.

Occurrence.—Pools at Makthlawaiya.

PARALIMNETIS, gen. nov.

Male.—Structure as in *Limnetis*, but with following differences:—first pair of legs alike, with stem greatly reduced and prehensile organ very large; second pair greatly modified and dissimilar.

PARALIMNETIS RAPAX, sp. n.

Male.—Shell nearly circular; length 4 mm.; greatest height 3.4 mm. Surface marked with clear lines radiating from the shell-gland and anastomosing. Seen from above the greatest width of the two valves is about four-fifths of their length, and they do not taper at either end.

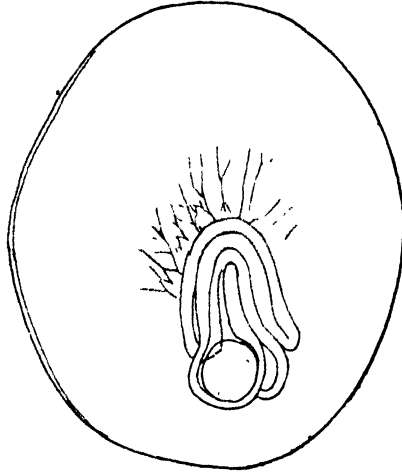
In side view the head and rostrum form an evenly arched curve, truncated at the end where the fornix broadens out into a shovel-shaped tip. Seen from in front the median ridge divides towards the end of the rostrum, so that the distal end is hollowed out and has a slightly concave margin.

The first pair of legs are alike and modified into relatively enormous clasping organs. The stem is very much reduced and bears only two small endites, the proximal one corresponding to the gnathobase. There is in all Conchostraca a tendency to a reduction of the endites on the first leg of the male. In *Estheria* it seems that the third and fourth endites of the normal appendage are fused, and that the large first joint of the clasper corresponds to the fifth endite (not to the fourth and fifth, as Borradale represents it). In *Limnetis* the stem between the gnathobase and the clasper is fringed evenly with setæ, and there is no separation of endites at all. In the present species the reduction has gone still further, and there

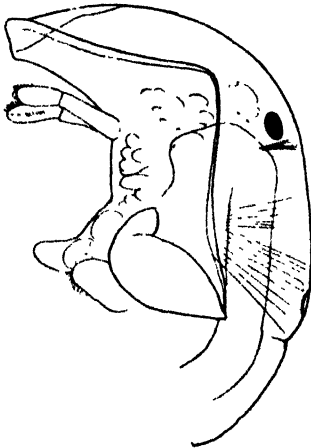
remains only a quite small curved lobe between the gnathobase and the clasper to represent endites 2, 3, and 4.

The clasper with the claw closed has an almost circular outline. The basal joint is broader than long, its inner margin evenly rounded, and the

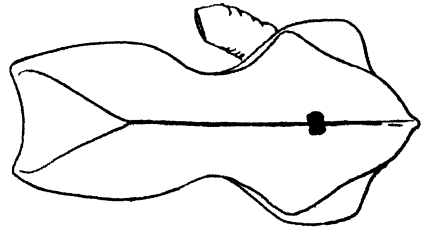
TEXT-FIG. 17.



TEXT-FIG. 18.



TEXT-FIG. 19.



Paralinnnetis rapax, sp. n. Male.

Fig. 17.—Right shell. Fig. 18.—Side view of head.

Fig. 19.—Front view of head.

distal free margin straight, with a few small teeth at its inner angle. It bears two palps, each fringed with long setæ. The terminal claw is very large, broad at the base, and hollowed out along its inner face,

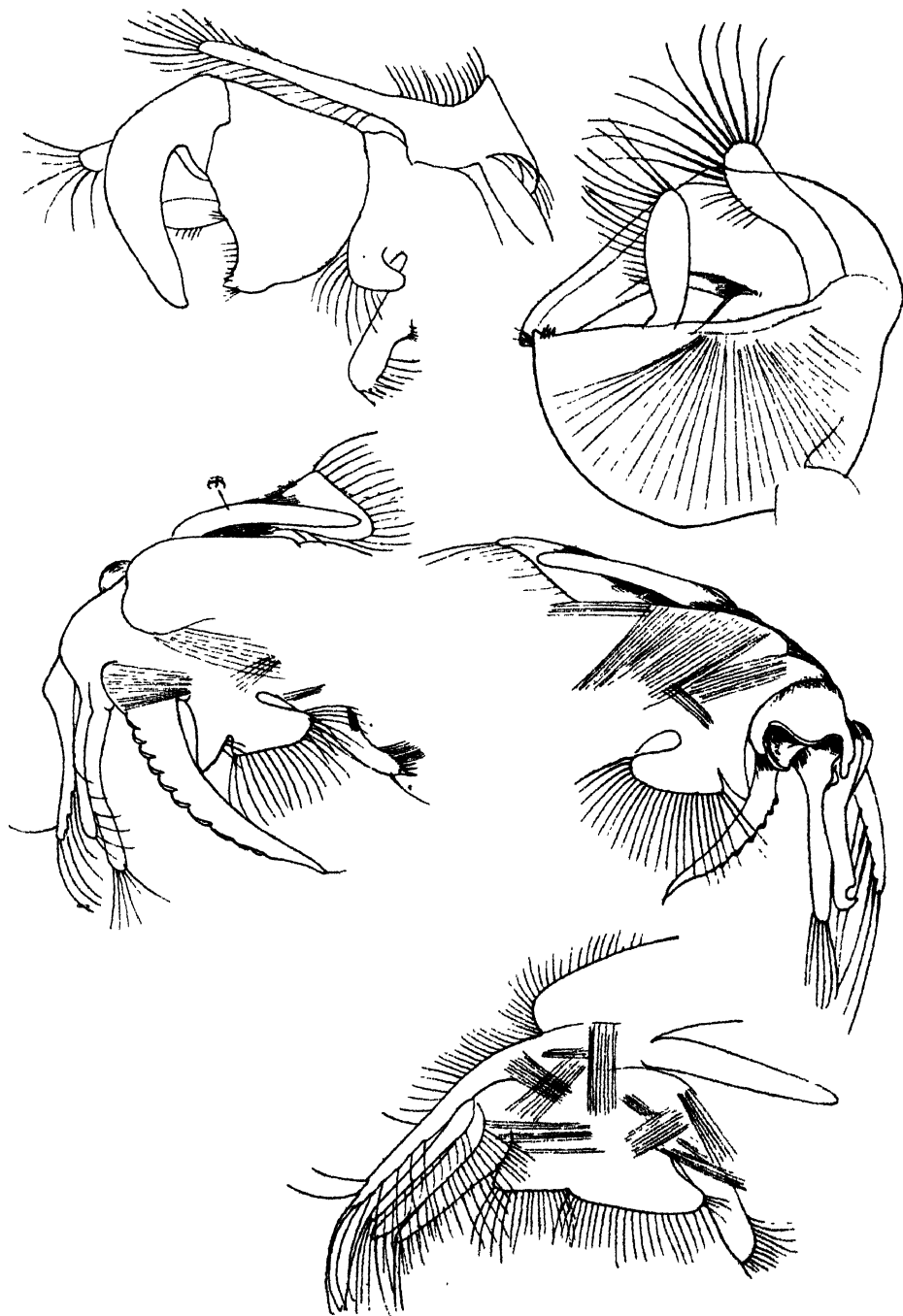
*Paralimnetis rapax*, sp. n. Male.

Fig. 20.—Leg 1 of right side.

Fig. 21.—Clasper of leg 1, left side.

Fig. 22.—Leg 2, right side.

Fig. 23.—Leg 2, left side.

Fig. 24.—Leg 8.

The second leg, which in *Limnetis* resembles the succeeding pairs, is here much modified, and the two legs of the pair are unlike each other. In both legs the six endites of the normal Conchostracan appendage are recognizable, but the third is very small and almost without setæ, while the fourth is a large sickle-shaped structure with a series of notches on its distal curved edge. It is sharply pointed at the end, where a single small hair is inserted.

Endites 5 and 6 are long, slender processes. On the right side both are simple and bear setæ at the end, but on the left side the sixth endite has no setæ and has a hook-like end. In this appendage also the part of the stem corresponding to endites 4 and 5 is expanded on the outer side into a peculiar structure which is difficult either to describe or to draw. It seems that the outer edge of the stem is broadened out into a thick chitinous plate which curves over towards the inner side, and its free proximal part forms a blunt claw. At the base of the modified fourth endite there is a V-shaped ridge on the stem, which seems to form a pad on to which the outer plate may press.

There are ten pairs of legs.

The telson is simply rounded at the end, with a number of short hairs.

Occurrence.—Pool at Makthlawaiya, 11. xii. 26.

Reports of an Expedition to Brazil and Paraguay in 1926-7, supported by the Trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for Scotland.

Microlepidoptera. By E. MEYRICK, B.A., F.R.S.

(Communicated by Dr. G. P. BIDDER.)

[Read 3rd January, 1929.]

I AM indebted to Dr. G. S. Carter for the opportunity of examining the following material, representing his captures at Makthlawaiya in the Chaco region. It is probable that the locality is not of a character to be very productive in this particular group; however, twenty-two of the species are new to science. So far as can be judged from these samples, the fauna would seem to be of the same general type as that of the valley of the Amazon.

PTEROPHORIDÆ.

ADAINA NAIADOPA, sp. n.

♂ ♀. 13-14 mm. Head pale greyish-ochreous, fillet white. Palpi ♂ 1, ♀ 1½, white. Thorax and abdomen whitish. Forewings white; cloudy grey dots at base of cleft and on costa beyond this; minute blackish dots on apex of segments, and of vein 7; cilia white. Hindwings whitish-grey; cilia whitish.

2 ex., May.

STENOPTILIA TRIGONOMETRA, sp. n.

♂ ♀. 12-14 mm. Head white. Palpi 2, white, second joint grey except apex. Thorax whitish. Forewings cleft to $\frac{2}{3}$, segments moderate, first acute-pointed, second with termen very oblique; light brownish-grey, speckled white, irregularly sprinkled dark fuscous; a well-marked dark fuscous dot in disc at $\frac{1}{3}$, and two transversely placed near before base of cleft and rather above and below it; a short linear dark fuscous mark on costal edge above these latter, and a smaller one before middle of first segment, separated by white suffusion; cilia pale greyish, on costa and apex white with a greyish bar on second costal mark, beneath apex with a blackish-grey dot, on termen of second segment somewhat mixed dark fuscous at base. Hindwings dark grey; cilia grey.

2 ex., November, January. Allied to *S. insperata*.

EUCOSMIDÆ.

BACTRA VERUTANA Zell.

2 ex., November, December. Widely distributed in N. and S. America.

G E L E C H I A D Æ.

TRICHEMBOLA IDIARCHA, sp. n.

♂. 14–16 mm. Head and thorax white. Palpi dark brown, terminal joint and hairs of upper edge of second white. Forewings elongate, costal gently arched, apex obtuse, termen obliquely rounded; ochreous-whitish, becoming white towards costa anteriorly, more brownish-tinged posteriorly, some scattered fuscous and dark fuscous specks, sometimes some dark irroration towards termen; costal edge dark fuscous towards base; stigmata small, black, plical obliquely before first discal, in one example first discal absent; sometimes minute blackish dots above fold at $\frac{1}{3}$ and towards costa at $\frac{1}{3}$; cilia light brownish, more whitish on costa and beneath tornus. Hindwings light grey; cilia whitish-ochreous.

6 ex., October to February. This is the first American species of the genus, the other six being all Asiatic.

ARISTOTELIA PELTOSEMA Low.

2 ex., October, November. Although the larval habits are not yet known, this widely distributed insect is evidently carried by man with some cultivated plant.

SYNACTIAS, gen. nov.

Head with appressed scales; ocelli posterior; tongue developed. Antennæ $\frac{4}{5}$, scape elongate, without pecten. Labial palpi very long, recurved, second joint with appressed scales, terminal joint as long as second, slender, acute. Maxillary palpi very short, filiform, appressed to tongue. Posterior tibiæ clothed with loosely appressed hairs above. Forewings 2 from angle, transverse vein very oblique, 3 parallel, 4 and 5 connate, 7 and 8 stalked, 7 to costa, 11 from middle. Hindwings $\frac{4}{5}$, elongate-trapezoidal, apex pointed, termen sinuate, cilia nearly 2; 3 and 4 nearly approximated at base, 4 and 5 connate, 6 and 7 rather approximated towards base.

Probably belongs to the group of *Recurvara*.

SYNACTIAS MICRANTHIS, sp. n.

♀. 9 mm. Head ochreous-whitish, face pearly-whitish. Palpi whitish, basal half of second joint dark grey. Thorax whitish-ochreous, tegulæ blackish. Forewings lanceolate; blackish; a narrow irregular-edged ochreous-whitish costal streak from base to apex; a rather broad light ochreous-yellow dorsal streak from base attenuated to tornus, upper edge white, with an excavation about middle of wing; terminal edge ochreous-whitish; a fine transverse ochreous-whitish strigula near apex (cilia denuded). Hindwings pale greyish; cilia ochreous-grey-whitish.

1 ex., May.

TELPHUSA PENETRATRIX, sp. n.

♀. 19 mm. Head and thorax grey suffusedly mixed white and sprinkled blackish. (Palpi broken.) Forewings rather narrow, apex tolerably pointed, termen very obliquely rounded; grey irrorated dark grey and blackish; a slight black longitudinal mark beneath costa at base, from beneath this an irregular black fasciate streak dilated on lower part to dorsum at $\frac{1}{3}$, on fold with some raised scales and acute projections on each side; an oblique series of three suffused black spots from beneath costa at $\frac{2}{3}$ to fold, some white marking on fold between this and preceding; from beyond this in disc a rather thick blackish streak runs to apex, interrupted on end of cell with some white scales; an obscure whitish angulated transverse shade at $\frac{3}{4}$, interrupted by the black longitudinal streak; cloudy dark fuscous marginal dots round apical part of costa and termen, surrounded with white irroration; cilia pale greyish sprinkled black and barred whitish. Hindwings grey, darker terminally; cilia pale grey, whitish towards tips.

1 ex., October.

GELECHIA SPIRODOXA, sp. n.

♀. 11 mm. Head white, slightly sprinkled grey. Palpi blackish, terminal joint whitish with two blackish bands. Thorax grey mixed and partly suffused white. Abdomen dark fuscous with white segmental rings, broader beneath. Forewings blackish; base narrowly and irregularly white; rather narrow somewhat irregular oblique white fasciæ at $\frac{1}{4}$ and middle; a small cloudy white spot on costa at $\frac{3}{4}$, and indistinct whitish marginal dots from this round costa and termen to tornus; cilia white. Hindwings and cilia grey.

1 ex., May. Belongs to the group of *albitorella*.

GELECHIA PERTINENS, sp. n.

♀. 12 mm. Head whitish-ochreous sprinkled fuscous. Palpi whitish, second joint sprinkled dark fuscous, with blackish subapical and subbasal bands, terminal joint as long as second, with blackish subbasal ring. Thorax fuscous, pale-sprinkled, shoulders suffused dark fuscous. Forewings apex obtuse-pointed, termen very obliquely rounded; fuscous sprinkled dark fuscous; two or three white scales scattered on fold, plical stigma moderate, blackish, edged with some white scales posteriorly; second discal stigma blackish, connected by a suffused blackish streak with apex; cilia whitish-fuscous sprinkled dark fuscous. Hindwings 1, termen slightly sinuate; grey; cilia light greyish.

1 ex., May.

STEGASTA COMISSATA Meyr.

3 ex., February to May. Also from the Lower Amazon.

STEGASTA SCOTEROPIS, sp. n.

♂. 8 mm. Head grey sprinkled blackish, forehead whitish, face whitish-ochreous. Palpi white, second joint irrorated black, terminal joint with subbasal ring and broad subapical band of black irroration. Thorax grey irrorated blackish. Forewings grey-whitish closely irrorated dark fuscous, appearing dark grey; a blackish transverse streak from costa at $\frac{1}{3}$ reaching $\frac{2}{3}$ across wing; rather broad blackish transverse fasciæ before and beyond middle not reaching dorsum, first terminated beneath by a bent longitudinal black partly raised mark edged with some white scales, second including black second discal stigma edged above by an ochreous dot, on margins of these fasciæ two or three silvery-whitish scales towards costa: cilia grey-whitish speckled black. Hindwings dark grey, thinly scaled and subhyaline in disc; cilia grey; costal hair-pencil yellow-whitish, fold pale yellow. Forewings and hindwings beneath blackish-scaled except posteriorly.

1 ex., May.

PHTHORIMÆA OPERCULELLA Zell.

Common, October–May. This highly injurious pest of the potato, now very widely spread, was doubtless introduced with its food-plant.

PHTHORIMÆA ARDEOLA, sp. n.

♂. 9 mm. Head and thorax ochreous-whitish. Palpi ochreous-white, second joint with two rings of blackish irroration. Forewings yellow-ochreous, with scattered black specks, suffusedly lined or streaked whitish on veins, costal area wholly suffused whitish except at base, where is a group of black specks; a narrow line of black irroration from end of cell to apex, strongest at apex (cilia denuded). Hindwings pale blue-grey; cilia ochreous-whitish; a very large expansible ochreous-whitish hair-pencil from base of costa directed along it.

1 ex., May. This and the next species are both allied to the preceding, and therefore probably also attached to Solanaceæ.

PHTHORIMÆA ISOCHLORA, sp. n.

♂. 9 mm. Head, palpi, thorax ochreous-whitish. Forewings ochreous-whitish; a very faint greyish tinge towards apical part of costa: cilia ochreous-whitish. Hindwings very pale blue-grey; cilia ochreous-whitish; an expansible whitish-ochreous hair-pencil from base lying along costa.

1 ex., May.

ANACAMPSIS FLEXILOQUA Meyr.

1 ex., May. Also from the Upper Amazon, Peru.

GLYPHIDOCERA TRACHYACMA, sp. n.

♂. 13 mm. Head and thorax whitish-grey-ochreous, some dark fuscous specks. Palpi ochreous-whitish, irrorated dark fuscous except towards apical third of joints, much thickened with scales, terminal joint with scales roughly projecting posteriorly. Antennæ stout, subbasal excavation rather large, scaled above. Forewings elongate, somewhat dilated, termen rather oblique, slightly rounded; 8 and 9 stalked; fuscous, whitish-sprinkled, some scattered dark fuscous scales; stigmata moderate, cloudy, blackish, plical obliquely before first discal; terminal and apical area suffused darker fuscous; a terminal series of blackish scales: cilia pale greyish, two dark grey shades. Hindwings whitish-grey; cilia light grey.

1 ex., October. The projecting scales of terminal joint of palpi are a peculiar character, but need not involve generic separation, the species being a true *Glyphidocera* in all other respects.

ECOPHORIDÆ.

MACHIMIA HELOBLA, sp. n.

♂, 17-18 mm.; ♀, 23 mm. Head and thorax white. Palpi white, second joint externally dark grey except apex. Antennal ciliations ♂ 1½. Forewings elongate, not dilated, costa gently arched, termen rather obliquely rounded, ♀ more oblique; shining white: cilia white. Hindwings white tinged grey; cilia white.

3 ex., November to February. Superficially strongly resembles a *Schmœbius*.

MACHIMIA MORATA Meyr.

2 ex., October, December. Also from Parana, Argentina.

XYLORYCTIDÆ.

STENOMA DEUTEROPA, sp. n.

♀. 16 mm. Head and thorax white. Palpi white, second joint fuscous except apex. Forewings oblong, costa anteriorly moderately arched, then straight, apex obtuse, termen straight, vertical; all veins separate, 8 to costa; white; triangular blackish spots on costa before middle and at ¾; second discal stigma moderately large, blackish; three or four minute blackish marginal dots round apex (cilia denuded). Hindwings with veins normal; whitish; cilia white.

1 ex., May. Near *S. notifera*.

STENOMA DRYAULA Meyr.

1 ex., May. Also from Lower Amazons.

COSMOPTERYGIDÆ.

PRECHOLA HOLOMORPHA, sp. n.

♂. 14 mm. Head, palpi, thorax dark purplish-fuscous. Forewings dark purplish-bronzy-fuscous: cilia grey. Hindwings light grey; cilia whitish-grey-ochreous, becoming light grey on costa.

1 ex., November.

SCYTHRIDÆ.

SCYTHRIS DIMOTA, sp. n.

♂ ♀. 12 mm. Head and thorax bronzy-fuscous, some white scales on posterior edge of thorax. Palpi dark fuscous, basal joint and base of second ochreous-white. Abdomen dark fuscous, ♂ beneath ochreous-white towards apex, ♀ beneath ochreous-white except last two segments. Forewings dark purplish-fuscous; a white streak along fold from base to near middle of wing, ♂ thicker and irregular, and its apex connected with dorsum by irregular white suffusion; some cloudy white suffusion about end of fold and tornus: cilia rather dark grey. Hindwings 3, 4 and 5 separate; dark fuscous; cilia rather dark grey.

2 ex., May.

SCYTHRIS DEPRESSA, sp. n.

♂. 11 mm. Head and thorax dark purplish-grey, sternum white. Palpi dark grey, basal joint and basal half of second white. Abdomen blackish, anal tuft grey segmental margins on ventral surface pale ochreous-grey. Forewings dark purplish-grey; a few whitish scales on fold towards middle: cilia grey. Hindwings 3, 4 and 5 separate; dark grey; cilia grey.

1 ex., November.

SCYTHRIS PLOCOGASTRA, sp. n.

♀. 12 mm. Head and thorax purplish-grey, irregularly mixed white. Palpi dark grey sprinkled white, base white. Abdomen blackish, thickly strewn with white hair-scales, anal segment whitish, ventral surface wholly suffused white, apex ochreous-yellow. Forewings purplish-grey speckled dark fuscous and sprinkled whitish: cilia pale grey. Hindwings dark grey; cilia grey.

1 ex., May.

COLEOPHORIDÆ.

COLEOPHORA LEPTYROPIS Meyr.

10 ex., December to May. Also from the Lower Amazon. The ground-colour of the forewings may more properly be termed white, and the very indefinite suffusion ochreous-yellowish. Terminal joint of palpi erected nearly at right angles to second.

COLEOPHORA ZYMOTICA, sp. n.

♂. 8-9 mm. Head, palpi, thorax whitish, palpi simple, straight. Antennæ simple, white, ringed pale ochreous. Forewings yellow-ochreous, minutely grey-sprinkled; costal edge to beyond middle, and all veins marked with white lines, rendered slightly irregular by the grey speckling; cilia whitish. Hindwings light grey; cilia grey-whitish.

2 ex., November. Allied to *C. lepyropis*.

HYPONOMEUTIDÆ.

PERISCEPTIS, gen. nov.

Head (rubbed, probably with appressed scales); ocelli posterior; tongue absent. Antennæ $\frac{3}{2}$, stout, simple, scape moderate, with pecten. Labial palpi moderate, porrected, second joint with appressed scales, terminal joint half second, subascending, scaled, tolerably pointed. Maxillary palpi absent. Posterior tibiæ with appressed scales. Forewings 1 *b* short-furcate, 2 from $\frac{1}{2}$, 3 from angle, 4 absent, 7 to costa, 8 absent, 11 from somewhat before middle. Hindwings 1, subovate, cilia $\frac{1}{2}$; 2 remote, 3 from angle, 4 absent, 5-7 somewhat approximated towards base.

Probably allied to the *Ethmia* group.

PERISCEPTIS HORIARCHA, sp. n.

♂. 13 mm. Thorax whitish-grey. Forewings elongate, rather dilated, costa moderately arched, apex rounded, termen rounded, somewhat oblique; grey-whitish; about seven small rather dark fuscous spots along costa (one beyond middle largest), about six dots round apical and terminal margin, one in disc on end of cell, and one or two small strigulæ above dorsum; cilia whitish. Hindwings pale greyish; cilia grey-whitish.

1 ex., December.

PLUTELLIDÆ.

PLUTELLA MACULIPENNIS Curt.

Common, October, November. This cosmopolitan insect is introduced with cultivated *Brassica*.

TINEIDÆ.

ACROLOPHUS CORRIENTIS Wals.

1 ex., December. Ranges from Colombia to Argentina.

ACROLOPHUS CYCLOPHORA, sp. n.

♂. 16-17 mm. Head and thorax ochreous-whitish more or less mixed dark fuscous. Palpi extremely long, strongly recurved, reaching to end of thorax, ochreous-whitish, on outer side partially and irregularly mixed dark fuscous. Antennæ lamellate-pectinated ($2\frac{1}{2}$). Uncus moderate, slightly

curved, single, slender, acuminate; valva straight, narrow, elongate, gradually dilated, apex rounded. Forewings elongate, costa gently arched, termen rather obliquely rounded; 7 and 8 stalked; whitish-grey-ochreous, irregularly sprinkled fuscous, especially towards margins; some dark fuscous irroration forming strigulae or small spots towards costa and dorsum, several more distinct small dark spots on costa towards apex; a round fuscous spot or dot below fold at $\frac{1}{4}$; a large oval dark fuscous spot on fold in middle of wing, and a smaller round spot in disc at $\frac{2}{3}$; some irregular small dark fuscous dots towards termen: cilia ochreous-whitish, irrorated dark fuscous at base and on outer half, tending to form obscure bars. Hindwings rather dark grey; cilia grey-whitish.

2 ex., November.

ACROLOPHUS LEUCOTRICHA, sp. n.

♂. 14 mm. Head white. Palpi very long, strongly recurved, with very long rough spreading hairs anteriorly, those at apex reaching middle of thorax, white, slightly sprinkled grey externally, with grey bar from apex of basal joint. Antennae biciliated (1). Thorax white, tegulae sprinkled grey towards apex. Uncus apparently imperceptible; valva short, straight, very narrow throughout, apex somewhat swollen and rounded. Forewings elongate, costa gently arched, termen rather obliquely rounded; 7 and 8 stalked; ochreous-whitish, some minute irregularly scattered fuscous specks; costal edge infuscated on basal third; stigmata obscurely indicated by undefined groups of minute dark fuscous specks, discal remote, plical slightly beyond first discal; five dots of minute dark fuscous specks on costa towards apex: cilia white, some dark fuscous specks towards base and tips, especially on median area of termen. Hindwings light grey; cilia grey-whitish.

1 ex., May. Probably allied to the preceding species.

ACROLOPHUS MONOCTENIS, sp. n.

♂. 16 mm. Head and thorax grey mixed whitish. Palpi extremely long, strongly recurved, reaching to beyond middle of thorax (denuded). Antennae unipectinated (2). Uncus double, widely separated at base, long, strap-shaped, bent down at right angles in middle, apical halves slightly sinuate, meeting at tips; valva strongly depressed, narrow at base but rather rapidly dilated, apex obtuse. Forewings moderate, rather narrowed towards base, costa moderately arched, apex rounded, termen rather obliquely rounded; 8 and 9 stalked; grey, sprinkled dark grey (largely denuded). Hindwings blackish-grey; cilia grey.

1 ex., May. Notwithstanding the denuded condition of the forewings (probably always obscure in colouring), the species is abundantly distinguished by the structural characters (in part unique), and cannot be mistaken.

Reports of an Expedition to Brazil and Paraguay in 1926-7, supported by the Trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for Scotland.

Amphibia and Reptilia. By H. W. PARKER, B.A.

(PLATE 16.)

[Read 3rd January, 1929.]

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THE author is indebted to Dr. G. S. Carter for the opportunity of studying a collection of reptiles and amphibians made by him in the Paraguayan Chaco. The collection contains representatives of twenty-five species, but, as none of these are new to the region, it does not appear necessary to publish a complete list. Nanahua and Makthlawaiya, the two localities in which the specimens mentioned below were collected, lie at 23° 30' S. by 59° 30' W., and 23° 25' S. by 58° 19' W. respectively. The accompanying figures were drawn by Lt.-Col. W. P. C. Tenison, to whom the author wishes to express his gratitude.

A. OPHIDIA.

LEIMADOPHIS [*LIOPHIS*] *PŒCHLOGYRUS RETICULATUS*, subsp. n.

The single half-grown female from Makthlawaiya (collected 30.iv.27) has the same colouring as the specimens from Rio Apa, Urucum, and Carandasinho, Paraguay, mentioned by Peracca*. In addition, nine specimens of this snake from Sta. Cruz, Bolivia, and one from Esperanza, E. Bolivia†, exhibit this same colour-pattern, which has not been noticed elsewhere in the area occupied by the species. In adults the belly and the two outer rows of dorsal scales are almost or completely immaculate white, the remaining dorsal scales being bluish-olive at the base and edged with black. Juvenile and some half-grown individuals show traces of the typical coloration of the species, the belly being more or less blotched with black and the dorsum with suggestions of irregular transverse dark bars. Specimens in the British Museum from Trinidad (N. Bolivia), Resistencia (Argentina), Asuncion (Paraguay), and Matto Grosso show an intermediate colour-pattern; the belly is often blotched with black; the dorsum, though having black-edged scales, has also irregular darker areas, and the ground-colour of the upper surface usually extends over the two outer scale-rows. It appears, therefore, that in S.E. Bolivia and N.W. Paraguay the normal

* Peracca, Boll. Mus. Torino, x, 1895, p. 14; *op. cit.* xix, 460, 1904, p. 7.

† Procter, Ann. Mag. Nat. Hist. (9) vii, 1921, p. 190.

adult *Leimadophis pœcilogyrus* is of a colour-variety which does not occur elsewhere, but which intergrades with the typical form in the intermediate areas; juvenile and half-grown specimens of this subspecies (*reticulatus*) may retain to a greater or less degree the colouring of the typical form, which must accordingly be also regarded as the more primitive.

B. LACERTILIA.

PANTODACTYLUS SCHREIBERSII ALBOSTRIGATUS (Griffin).

Prionodactylus albostrigatus Griffin, Ann. Carnegie Mus. xi, 1917, p. 314, pl. 34.

♂ and ♀, Makthlawaiya (collected 15. ii. 27 and 27. x. 26).

Though no typical or topotypical material of Griffin's species is available for comparison, the above-mentioned specimens, together with seven others from Bolivia and one from 'Brazil,' in the British Museum, agree so well with the original description that there is little doubt that they are the same form which Griffin had before him. (Comparison of these with a series of eighteen specimens of *Pantodactylus schreibersii* (Dum. & Bibr.) from various localities fails to reveal any constant structural differences, and also shows that the characteristic colour-pattern of *albostrigatus* may be indicated in specimens of *schreibersii*. The characteristic marking of *albostrigatus* is a white stripe from below the eye, through the ear, above the limbs, and along the tail; with this are associated white, black-edged ocelli on the fore-limb and the hinder side of the thighs. These markings are well developed on the female from 'Brazil,' and on six males from Bolivia (Sta. Cruz and Trinidad) and Paraguay (Makthlawaiya), but on three females from this region (Sta. Cruz and Makthlawaiya) the light line is well developed only on the head and neck. Three other females from Bolivia (Caiza) and N. Argentina (Jujuy) have this streak indicated on the head and neck by a series of white-tipped scales, but have lost the white ocelli; males from N. Argentina (Tucuman) and Rio Grande do Sul also show traces of the white streak in the region of the ear-opening, but in other specimens from Uruguay (4 ♀♀), Monte Video (♂ & 2 ♀♀), Rio Grande do Sul (5 ♀♀), and La Plata (♂) all traces of the light streak are lost. "*Prionodactylus albostrigatus*" must accordingly be regarded as a subspecies of *Pantodactylus schreibersii*, with a range from E. Bolivia and N.W. Paraguay to Minas Geraes.

C. AMPHIBIA (ANURA).

1. LEPTODACTYLUS DIPTYX Boettger.

Leptodactylus bufonius (in part.), Boulenger, Ann. Mag. Nat. Hist. (6) xiii, p. 348 (1894); Budgett, Quart. J. Micr. Sci. xlii, 1899, p. 306.

Examination of the four co-types of *Leptodactylus bufonius* Boulenger shows that the two smaller specimens are really *L. diptyx* Boettger; as,

however, the diagnosis of *L. bufonius* was undoubtedly based on the larger specimens, the name must be retained for the species to which they belong. It seems probable that Budgett may have fallen into the same error, as, in recording *L. bufonius* from Paraguay (*loc. cit. supra*), he states that he never found large specimens calling, but that the individuals whose call he describes were all small; he suggests that in *L. bufonius* there are either two varieties—a large and a small one—or that juveniles have the habit of calling. By analogy with other species neither of these suggestions seems probable. Breeding males of *L. bufonius* and *L. diptyx* have, apart from a general similarity in colour and habitus, one salient feature in common; in both the snout is extremely prominent, with a sharp horizontal edge, and it appears possible that this resemblance may have led to confusion in the field. The Museum of Zoology, Cambridge, formerly possessed five specimens of *L. bufonius* presented by Budgett, and of these the two remaining undoubtedly belong to that species; as, however, Budgett definitely states (*loc. cit.*) that “only one specimen was secured,” the Cambridge specimens may have been obtained at a later date.

2. CERATOPHRYS [LEPIDOBATRACHUS] LEVIS (Budgett).

Boulenger * has pointed out that *Lepidobatrachus* cannot be satisfactorily differentiated from *Ceratophrys* (*sensu lato*); the half-grown specimen in the present collection (collected at Nanahua, 20. i. 27) gives no further evidence in favour of such a differentiation, but the highly modified tadpole described below suggests that, when sufficient osteological material is available, differences may be found which will warrant the retention of *Lepidobatrachus* as a distinct genus. The vomerine teeth, shown by Boulenger (*loc. cit.*) to be present, are small and not ankylosed to the vomer in adults and not developed in half-grown individuals; their position is marked by two small prominences close to the inner front edge of the choanæ.

The two tadpoles (collected at Nanahua, Dec. 1926, by Mr. A. Pride) have the fore-limbs just developed, but retain the larval mouth-parts, and are almost certainly referable to this species or to *C. asper* (Budgett); the hind-limbs are *Ceratophrys*-like, with a single large metatarsal shovel, and the first digit of the fore-limb is distinctly shorter than the second, a character which distinguishes *C. levis* and *C. asper* from all the other species of *Ceratophrys* known from this area.

Description of Tadpole.—Head and body very strongly depressed, once and one-third as long as broad, twice and one-quarter as broad as deep; head flat above; nostrils close together, directed upwards, and twice as far from the end of the snout as from the eyes; the latter directed upwards, the distance between them greater than that between the nostrils; anus median; tail

* Ann. Mag. Nat. Hist. (9) iii, 1919, p. 531.

3½ times as long as deep, with subequal crests, the dorsal extending forwards very slightly on the body. Mouth subterminal, very broad, ¾ the width of the head; upper lip with a short fringe bearing a few (20) very small unequal lappets at its free edge; lower lip without a fringe, but bearing a single row of very small widely-spaced papillæ on its lower surface: mouth-opening occupying the whole of the oral area and bearing a single row of small conical teeth along both its upper and lower margins; these teeth are serrations of a continuous black horny base, and diminish in size laterally, merging into the basal piece at the corners of the mouth; the upper tooth-row somewhat longer than the lower and in front of it when the mouth is closed.

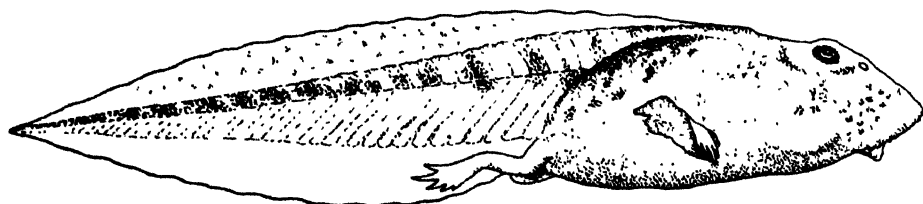
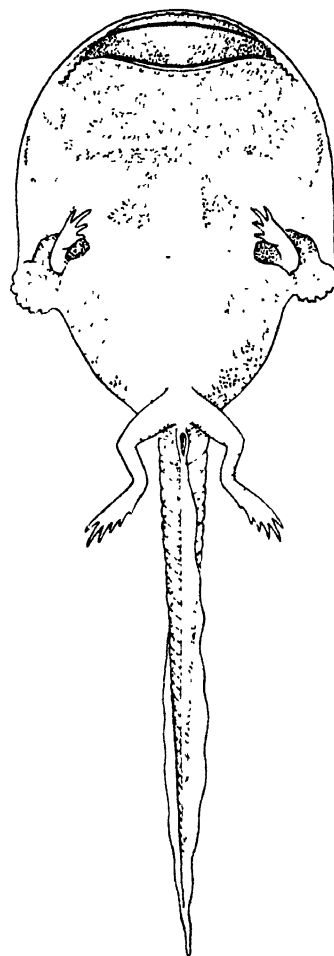
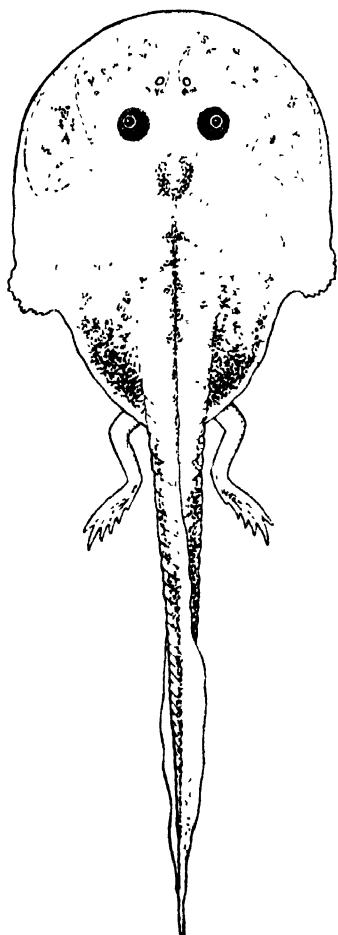
Colour in spirit.—Translucent, with irregular brown spots on the upper surface of the head and body and the upper caudal crest; the dorsal half of the muscular portion of the tail with a more or less continuous dark stripe; ventral caudal muscles and crest and lower surfaces of head and body immaculate white or with a few small black spots posteriorly.

Total length 92 mm.; head and body (measured to hinder side of thighs) 41 mm.; tail (measured to junction of lateral line with body) 57 mm.; head-width 32 mm.

The mouth-parts of this tadpole, which are unlike those of any other known, would appear at first sight to be as different from the ordinary Leptodactylid type, as, for example, those of a Brevicipitid. It appears probable, however, that the long tooth-rows are really homologous with the horny "beak" of a normal Leptodactylid or Ranid tadpole; transverse sections of a tooth-row show that it has essentially the same structure as, for example, the "beak" of the tadpole of *Rana temporaria*. An enormous enlargement of the larval mouth proper has taken place at the expense of what may be termed the vestibule of the normal tadpole mouth, with a corresponding lateral elongation and vertical weakening of the beak, and complete suppression of the rows of isolated teeth which are normally present on the vestibule.

Examination of the contents of the alimentary canal of one specimen shows that, as might be expected, the animal is essentially carnivorous, the food being ingested whole. The stomach contained thirty complete tadpoles of an average length of about 9 mm., two Conchostraca, and one beetle, whilst in the intestine, in addition to tadpole remains, were about fifty Conchostraca and the remains of an aquatic insect. Of the four other known tadpoles of the genus *Ceratophrys*, two (*C. americana* and *C. boiei*) appear to be omnivorous, and have no specialization of the mouth-parts, but the other two (*C. ornata* and *C. dorsata*) are definitely carnivorous, and the list of intestinal contents given by Noble * for a tadpole of *C. dorsata* bears a striking

* Noble, Ann. New York Ac. Sci. xxx, 1927, p. 83.



CERATOPHRYS LAEVIS.

similarity to the list given above. Both *C. ornata* and *C. dorsata*, however, have a large powerful beak, with which the prey is seized and bitten to a greater or less extent, and also a larger number of tooth-rows than the unspecialized species; in *C. boiei* and *C. americana* the number of tooth-rows is $\frac{2}{3}$ compared with $\frac{1}{2}$ in *C. ornata* and *C. dorsata*. Thus it appears that whilst the last-mentioned two species have acquired enlarged powerful cutting beaks and a greatly increased number of tooth-rows, *C. laevis*, in correlation with exactly the same type of food, has become modified in the reverse direction; the beak, though enormously enlarged, is weak and obviously of little value as a cutting organ, and the tooth-rows are entirely absent. Noble (*loc. cit.*) has stressed the fact that the size of the mouth and the number of tooth-rows may be very different in closely related species, but nevertheless it appears improbable that the mouth-parts of the larvæ of species of the same genus should have become modified to subserve the same function in two diametrically opposite directions. As has been suggested above, further material may show that the species *laevis* and *asper* ought to be referred to a separate genus.

EXPLANATION OF PLATE 16.

Tadpole of *Ceratophrys*, *Lepidobatrachus laevis* (Bodgett).

Reports of an Expedition to Brazil and Paraguay in 1926-7, supported by the Trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for Scotland.

The Oligochæta. By J. STEPHENSON, M.B., D.Sc., F.R.S.
(Communicated by Dr. G. P. BIDDER.)

(PLATES 17 & 18, and 2 Text-figures.)

Read 3rd January, 1929.

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I. INTRODUCTION

The following pages contain an account of the Oligochæta collected by Dr. G. S. Carter, of Glasgow University, and Mr. L. C. Beadle, of Pembroke College, Cambridge, in and near Makthlawaiya, lat. 23° 25' S., long. 58° 19' W., in the Chaco, the swampy region of N.W. Paraguay, during their prolonged residence there in 1926-7. I owe to Dr. Carter my thanks for the opportunity of examining this interesting collection.

Oligochæta from Paraguay have been made known to us as the result of collections made by Kerr (Beddard, '92), Borelli (Rosa, '95; Cognetti, '00), Jordan (Rosa, '95), Daday (Michaelsen, '05*a*), and des Arts (Cognetti, '07; Michaelsen, '17). Of these, Kerr and des Arts alone obtained specimens from the northern and more remote part of the country, from which the present specimens come (Kerr from the Pilcomayo, about 100 miles S. or S.E. of Makthlawaiya, des Arts from Puerto Max on the R. Paraguay, about 75 m. to the N.E.). As was therefore to be expected, the present collection contains a large proportion of new species. Limicoline forms are in the majority, as was also to be expected from the nature of the locality.

The list is as follows:—

Fam. *ÆOLOSONMATIDÆ*.

Gen. *ÆOLOSOMA*.

Æolosoma sp. i.

Æolosoma sp. ii.

- Fam. NAIDIDÆ.
 Gen. PRISTINA.
Pristina macrochaeta, sp. n.
 Gen. NAIS.
Nais paraguayensis Mich.
Nais pectinata Steph.
 Gen. AULOPHORUS.
Aulophorus carteri, sp. n.
Aulophorus borellii (Mich.).
Aulophorus beudlei, sp. n.
Aulophorus pectinatus, sp. n.
- Fam. TUBIFICIDÆ.
 Gen. LIMNODRILUS.
Limnodrilus chacoensis, sp. n.
- Fam. MEGASCOLECIDÆ.
 Subfam. OCNERODRILINÆ.
 Gen. KERRIA.
Kerria limosa, sp. n.
Kerria hortensis, sp. n.
Kerria pascuorum, sp. n.
- Fam. GLOSSOSCOLECIDÆ.
 Subfam. GLOSSOSCOLECINÆ.
 Gen. OPISTHODRILUS.
Opisthodrilus borellii Rosa.
 Gen. DIACHÆTA.
Diachæta exul, sp. n.
 Subfam. MICROCHÆTINÆ.
 Gen. DRILOCRIVUS.
Drilocrivus sp.

The examination of the limicoline Oligochaeta, especially the smaller forms, the Æolosomatidæ and Naididæ, is never easy in the case of preserved material. The beautifully transparent living bodies of these delicate worms become relatively opaque when preserved; the setæ, on the measurements and fine details of structure of which so much depends, lie usually in an unfavourable position for examination—not flat and in one plane—and their basal portions in the body-wall are obscured. Moreover, the usual fixatives employed in the laboratory for histological and cytological work cause much contraction and distortion; strong Flemming, for example, makes these delicate worms very dark and opaque, so that it is impossible to see any internal structure; Bouin's fluid seems to have caused the disintegration of the gills in some of the specimens of *Aulophorus*, and sublimate-acetic has corrugated and rendered irregular the palps of other specimens.

The best method of fixation for all ordinary purposes of morphology is that of *dilute* sublimate-acetic used hot, but some distance below boiling; 1 per cent. sublimate may be used for the larger species of Naididæ, and 0·1 per cent. (Piguet, '06) for the smaller; in this latter case presumably the heat is the chief fixative agent, but the results are excellent,

II. GEOGRAPHICAL DISTRIBUTION.

The genus *Æolosoma* and the commoner genera of Naididæ are cosmopolitan, and are pretty certain to be found in any region where conditions are suitable and thorough examination is made. It is interesting to note the predominance of *Aulophorus* and the absence of the closely related *Dero* in the present collection; there is no obvious reason for either peculiarity. Another point which is perhaps worthy of notice is that while none of the other Naididæ have so far been found outside Paraguay or the neighbouring part of Brazil, the two species of *Nais* are found also in India. *Nais paraguayensis*, first described by Michaelsen ('05 a) as occurring in Daday's collection from Paraguay, is one of the common Naididæ of India, where it has given rise to two varieties; it has been found also at Zanzibar. *Nais pectinata*, a not uncommon Indian worm, is now recorded for the first time from Paraguay; it has not so far been found in any intermediate locality.

These instances of a widely scattered distribution recall other similar occurrences. Many species of *Nais*, *Chætogaster*, *Pristina*, *Aulophorus*, and *Dero* are found in Europe and in India; the genus *Hæmonais* is at present known only from one locality in Switzerland and three places in India. It is possible, or even probable, that when the intermediate countries have been more thoroughly examined, these at present widely separated localities will be merged in a more or less continuous area of distribution.

The Tubificidæ to which family the genus *Limnodrilus* belongs, are predominantly a Northern Hemisphere group, and have rarely been recorded (twelve species) from regions south of the equator. The only South American representative of the family appears to be *Bothrioneurum americanum*; and the only records of the genus *Limnodrilus* from the Southern Hemisphere are *L. alpestris* Eisen (found originally in California) from S.W. Africa (Michaelsen, '14) and *L. lucasi* Benh., *L. rejzowskyanus* Benh., and a third, incompletely described species, from New Zealand (Benham, '03).

The characteristic "earthworm" genus of this region is the Oeneroдрiline *Kerria*, first collected not far from this same spot by Prof. Graham Kerr. It is not surprising, therefore, to meet with three species of the genus in the present collection. The interesting worm *Opisthodrilus borellii* is already known from North and Central Paraguay and from the Argentine Chaco. *Diachaeta* has hitherto been known only as a West Indian genus. *Drilocrius* has not hitherto been found nearer to Makthlawaiya than the State of São Paulo in Brazil.

III. SEXUAL MATURITY.

Neither the *Æolosomas* nor any of the Naididæ were sexually mature; but this is scarcely surprising, since reproduction in these worms is mainly asexual, by fission; the lack of sexual specimens causes no inconvenience to the systematist, since the discrimination of species is effected here on the basis of other characters.

But it is disappointing to find that the interesting worm, which belongs apparently to the genus *Drilocrius*, though collected on three separate occasions, is in no instance fully mature, and is therefore incapable of complete description and identification; it occurs in a region from which the genus has not previously been gathered, and is quite probably a new species. The Oligochaetes of marshes and swamps have sometimes, as probably here, a very restricted period of sexual maturity. Thus (Janda, '26) in Southern Moravia the sexual period of *Criodrilus lacuum* begins at the end of April and lasts till the end of June, being at its height in May; its whole duration is thus only two months. A similar state of things is well known in the species of *Alma*. Michaelsen ('15) draws attention to the fact that though *A. nilotica* is the common Oligochaete of Lower Egypt, we have but a scanty knowledge of the sexual processes of these worms; the sexual period is of restricted duration and falls within the hot season: only immature worms can be found in the cool weather, and, in fact, many gatherings of species of *Alma* contain only non-sexual specimens.

In the Egyptian *Alma* it seems likely that (at any rate, in certain localities) the whole generation of worms disappears annually, after becoming mature and copulating, by the drying up of the tanks and ditches in which they live (Michaelsen, *l. c.*). The cocoons, embedded in the dried mud, would then carry on the existence of the species through the hot weather. It is possible that something of the same kind happens in the case of the *Drilocrius* of the present collection; two of the three gatherings were made in October, another (and this the only one in which even a vestige of a clitellum was visible) in November; in another few weeks, when the hot season had advanced still further, it might conceivably have been possible to obtain fully sexual specimens. But Dr. Carter informs me that the marsh may dry up in any month, or for all months, or not at all; during the year of his residence it was only dry for a month, in March-April.

IV. THE GENUS *AULOPHORUS*.

Since the present investigation has brought to light several new species of *Aulophorus*, and so has considerably enlarged the genus, it may be convenient to give a conspectus of the several species in the form of a key. It is to be borne in mind that the characters are derived from descriptions of (for the most part) preserved and therefore contracted material; this must be remembered when it is a question of the length of the worm and the characters of the branchial fossa and gills.

- | | |
|--|--------------------------|
| 1. Dorsal setæ begin in segm. iv | <i>A. superterrenus.</i> |
| Dorsal setæ begin in v | 2. |
| Dorsal setæ begin in vi | 0. |
| 2. Two or three pairs of gills | 3. |
| Four pairs of gills | 4. |
| 3. Palps diverge at an obtuse angle | <i>A. furcatus.</i> |
| Palps close together, diverge but slightly | <i>A. africanus.</i> |

4. Dorsal needles pectinate	<i>A. pectinatus.</i>
Dorsal needles simply bifid	5.
5. Length 3-4.5 mm.; segms. ca. 50	<i>A. michaelseni.</i>
Length 20-35 mm.; segms. ca. 150	<i>A. borellii.</i>
6. Four pairs of gills	7.
Fewer than four pairs of gills	8.
7. Dorsal bundles of one hair and one needle seta	<i>A. beadlei.</i>
Dorsal bundles of two hairs and two needles, or three hairs and three needles	<i>A. graveleyi.</i>
8. Gills inconspicuous, one pair or rudimentary	<i>A. carteri.</i>
Gills well developed	9.
9. Length 8 mm. or more	<i>A. ragus.</i>
Length 4 mm. or less	10
10. Dorsal needles single-pointed	<i>A. stuhlmanni.</i>
Dorsal needles fan-shaped	11
11. Gills contained entirely within the fossa, ventral pair larger than the dorsal	<i>A. schmardai.</i>
Gills projecting from fossa; dorsal pair larger than ventral ..	<i>A. tonkinensis.</i>

I omit *A. palustris* Mich. (Michaelsen, '05 b), of which only a short preliminary diagnosis has appeared; the few details given by its author are now scarcely sufficient for adequate characterization, though, if I am right in supposing that by "Hakenborsten" (a term used by Michaelsen in describing the dorsal needles of this form) sigmoid crotchets similar to those of the ventral bundles are meant, their presence in the dorsal bundles would seem to distinguish the worm from all other species of the genus.

It is difficult to distinguish *A. tonkinensis* and *A. schmardai*; such differences as emerge from the diagnoses and descriptions of the two forms in Michaelsen's paper ('05 a) are for the most part small and perhaps within the limits of normal variability. Perhaps the best distinction is the form of the branchial fossa and gills.

Michaelsen ('14) has suggested a possible inaccuracy in the description of *A. stuhlmanni*: the dorsal needles, stated in the original account to be single-pointed, he thinks may really be fan-shaped, which, if true, would bring the species into line with the majority of forms with dorsal setæ beginning in segment vi. But it is, perhaps, unnecessary to suppose that the original description is erroneous—at any rate for the purpose of bringing *A. stuhlmanni* into line with the other forms with dorsal setæ beginning on vi; since there is another species in this group, *A. graveleyi*, in which the dorsal needles are not fan-shaped, but simply bifid, without a web between the prongs. In order to confirm my original statement (Stephenson, '25) I have re-examined my specimens, and find that there is not in fact any web between the prongs, and that therefore *A. graveleyi* also constitutes an exception to the rule of fan-shaped setæ in species of *Aulophorus* where the dorsal setæ begin in segment vi.

V. ON THE OCCURRENCE OF TWO FORMS OF CALCIFEROUS GLANDS (ŒSOPHAGEAL POUCHES) IN THE GENUS *KERRIA*.

In the three species of *Kerria* described in the present paper the calciferous glands appear in two distinct forms, represented in figs. 9 and 10 (Pl. 18). The glands of *K. hortensis* belong to the one type, those of *K. limosa* and *K. pascuorum* to the other.

In the first and simpler type (Pl. 18. fig. 9) a number of lamelliform longitudinal ridges (in *K. hortensis* about 20–25), formed simply by the folding of the lining epithelium of the pouch, project into the cavity. Between the two layers of the fold there extends a layer or lamella of blood—an extension from the sinus which lies, immediately external to the epithelial lining, in the sac-wall. In many or most of the lamellæ this extension of the blood sinus has a moniliform appearance in transverse section (*cf.* Pl. 18. fig. 9); this must be due to the fact that the blood in the lamellæ is contained mainly in a series of longitudinal channels which have only narrow and slit-like connections with their neighbours. The condition is very much the same as that in another worm described below—the widely removed Glossoscolecoid *Diacheta exul* (Pl. 18. fig. 12).

In the type of gland found in *K. pascuorum* (Pl. 18. figs. 10 *a*, 10 *b*) and *K. limosa* the œsophageal pouch is nearly solid; there is a small central lumen which extends throughout its length, narrow and slit-like or branched and star-shaped in transverse section. The thick walls are traversed longitudinally by a large number of blood-channels, circular in transverse section; the channels join together towards each end of the sac, so that the number becomes fewer, at the anterior end they unite into a single vessel, which attaches the extremity of the sac to the septum in front in the manner of a cord. The blood-channels seem at first glance to be arranged without obvious order; but on careful examination they are seen often—perhaps always—to form radial columns (*cf.* Pl. 18. fig. 10 *b*), more or less distinct and more or less regular. There are also seen in the transverse section a large number of minute empty spaces (*sp.*), invisible with the low power, which, like the blood-channels, have at first sight an irregular arrangement, but on closer inspection are seen, like them, to be disposed along radial lines; these lines alternate in general with the radial columns of blood-spaces. The minute spaces just described appear to be more numerous and regular towards the free extremity of the sac; they are scarcely or not at all visible near its origin from the œsophagus. Nuclei are numerous in the trabeculæ which separate the blood-channels, and in the layer which immediately surrounds the central lumen, but there is no definite epithelial lining to the cavity, nor are the minute spaces in the substance of the wall surrounded by an epithelial layer—indeed, they are often too small for this to be possible.

These two types of œsophageal pouch are known elsewhere in the subfamily Ocnero-drilinae, the first and simpler in, for example, the genus *Ocnero-drilus* (*cf.* the description in Stephenson and Prashad, '19), the second and more

complicated in *Gordiodrilus* (as described, for example, by Michaelsen, '13). Hence they may be called, as they are by Michaelsen, the *Ocnerodrilus* and *Gordiodrilus* types of structure.

It seems to me that we may explain the structure of the *Gordiodrilus* type by supposing it to have arisen from the simpler *Ocnerodrilus* type through an increase in the number of the lamellæ and their fusion side by side. A thick and solid wall would thus be produced; the spaces between neighbouring lamellæ are not, however, to be thought of as entirely obliterated—the last traces are seen in the minute empty channels or slits between the radial series of blood-vessels. We must suppose, in addition, that the peculiar mode of distribution of the blood in the lamellæ, which gives the moniliform appearance in transverse sections of the simpler type of gland, has developed to a further stage, and that the longitudinal blood-channels in the lamellæ are now for the most part cut off from their neighbours, instead of being joined by slit-like connections.

The internal structure of the sacs in species of the genus *Kerria* has not always been described by previous authors; we have no information as to the type to which belong those of *K. halophila*, *zonalis*, *asuncionis*, *papillifera*, and *stagnalis*. Those of *K. mcdonaldii* and *K. kukenthali* belong to the *Ocnerodrilus* type, those of *K. subundina* (= *K. borellii*), *garmani*, *eiseniana*, *rosæ*, and *saltensis* apparently to the *Gordiodrilus* type. In *K. gunningi** (Michaelsen, '13) the condition is intermediate between the two types of structure, and the same may possibly be the case in *K. rubra*.

It should be added that there are other types of calciferous glands besides these two in the *Ocnerodrilinæ*, as, for example, in *Paulistus* and *Kerriana*.

VI. SYSTEMATIC.

Family ÆOLOSOMATIDÆ.

Genus ÆOLOSOMA Ehrbg.

Though I do not name either of the species found in the present collection (if indeed they are distinct), I give a short description of each, since the genus has but seldom been recorded from South America.

Schmarda ('61) described *Æ. pictum*, now regarded as a *species inquirenda*, from Colombia; and Frenzel ('91) recorded, but with doubt (merely giving the name followed by a mark of interrogation), *Æ. quaternarium* from Cordoba in the Argentine. Though the occurrence of the genus is not doubtful, there is thus so far no fully characterized *Æolosoma* from the South American continent.

* According to Miss G. E. Pickford ("Synonymy in the Genus *Kerria* [Oligochæta, *Ocnerodrilinæ*]," *Ann. Mag. Nat. Hist.* (10) ii, p. 378, 1928), *K. gunningi* is identical with *saltensis*.

ÆOLOSONA sp. i.

1058. Makthlawaiya. 11. ii. 27. Three specimens, none sexual.

1060. Makthlawaiya. 26. iii. 27. A single specimen and two small fragments, none sexual.

The specimens are in length 1.4 mm. or thereabouts, in diameter 0.3 mm. A single zone of fission was present, behind the tenth segment ($n=10$); in the hinder animal (*i. e.*, the portion of the worm behind the fission-zone) there were five seta-bearing segments.

The prostomium is semicircular and slightly broader than the pharyngeal region, but not quite so broad as the main portion of the body.

In the preserved specimens the colour of the "oil-drops," a characteristic feature of the integument in the genus, is not to be made out; Dr. Carter informs me that no definite note was made of the colour in the living worms, but that Mr. Beadle, who actually collected and examined these specimens, is sure that they had no striking colour but were somewhat yellowish in tone.

The setæ are all capillary, and are 6, 5, 4 or fewer per bundle. They are of varying length, those of a bundle not approximately equal, but divisible roughly into longer and shorter; sometimes the setæ of a bundle are arranged in couples of one longer and one shorter, but there may be, for example, one long and four short setæ in a bundle. In length the longer setæ may reach 0.37 mm.; others measure 0.30 or 0.26 mm.; while the shorter ones are, as a rule, about 0.14–0.16 mm. long. The longest setæ are thus equal to or somewhat longer than the diameter of the (contracted and preserved) body; all are bowed slightly in a graceful curve; no serration is visible on the shaft; the longer setæ are considerably thicker than the shorter. On the average there appear to be fewer setæ in the dorsal than in the ventral bundles; the number in the dorsal bundles, though occasionally reaching six, may be as few as three, two, or one.

The œsophagus extends backwards to the level of the third setal bundle. A dilated portion of the gut, which may be named "stomach," follows, and takes up all but the last two of the ten segments of the anterior animal.

I could not see the cerebral ganglion. The nephridia begin in segment ii; I saw them in segments ii, iii, and x, but was unable to distinguish them in the intermediate segments.

In the absence of precise information as to the "oil-drops" in the living animal it is, unfortunately, impossible to say whether or not these specimens represent a new species.

ÆOLOSONA sp. ii.

1207. Swamp at Makthlawaiya. 26. iv. 27. A number of specimens, none sexual.

The worms show, as a rule, a single budding zone; such a specimen is from 2 to 2.3 mm. in length. The maximum diameter is 0.5 mm.; the middle region of the body is considerably thicker than the rest.

As in the previous species, the pigment ("oil-drops") has been dissolved out of the pigment-cells of the epidermis; there seems, however, to be a slightly greenish tinge about the worms. It is, perhaps, the pigment-cells which appear (especially in the prostomium) as empty round spaces; in addition, there are in the integument numerous other vacuoles, containing aggregates of granules which nearly fill them.

The budding zone ("zone of fission") occurs behind the tenth or eleventh setal bundles ($n = 11$ or 12).

The prostomium is rounded, and in most of the specimens presents a curious appearance, as if the alimentary canal, or a forward branch or diverticulum of it, were continued forwards as a narrow tube in the middle of the prostomium throughout its length. This, however, is due to a contraction and a consequent grooving of the under surface of the prostomium, which, when flat and well displayed, is seen to be semicircular in shape and fully as broad as the succeeding part of the body—indeed, a little broader than the pharyngeal region.

The setæ are all capillary, in both dorsal and ventral bundles, and are commonly four to six per bundle, but sometimes more or fewer: some are long, others shorter, so that here, as in the previous species, two groups can be distinguished. The longer setæ are 0.33, 0.36, or 0.4 mm. in length, the shorter often about 0.17 mm.; the shortest may be much less than half the length of the longest. Long and short occur in the same bundle, but not, as a rule, coupled or regularly alternating; thus, there may be in a bundle 3 long and 3 short, 2 long and 2 short, 4 long and 2 short, 3 long and 5 short, 3 long and 4 short: in a bundle having the latter constitution there was a regular alternation of long and short setæ. All are straight, not curved or bowed.

A groove is continued outwards on each side from the corner of the mouth. The buccal cavity (or pharynx) is thick-walled, tubular, and ascends vertically; the œsophagus is thrown into undulations and ends at the level of the third setal bundle.

The cerebral ganglion is not distinguishable.

The first nephridium is behind the first setal bundle, *i.e.*, it opens to the exterior in segment iii, to which segment it belongs.

There is here also no precise information regarding the colour of the "oil-droplets" during life. The anatomical characters are not very different from those of the preceding species; it has, however, a quite different facies under the microscope, though how far this is due to differences in fixation or in physiological condition at the time of fixation I cannot say.

Family NAIDIDÆ.

Genus PRISTINA Ehrbg.

PRISTINA MACROCHÆTA, sp. n.

276. Lagoon 5 m. E. of Makthlawaiya. 27. x. 26. Three specimens, none sexual.
1208. Makthlawaiya. 27. iv. 27. Several specimens, none sexual.

Length (exclusive of proboscis) 1.6 mm.; average diameter ca. 0.12 mm.

Segments of a single animal 21; in this specimen there was no budding-zone, but the last six segments were smaller and shorter, as if there had been originally a budding-zone behind segment xv. In other specimens a budding-zone occurs behind segments xvi, xv, xiv, xiii (?), or xii ($n=12$ to 16).

Much foreign matter adheres to the surface, but does not form a regular sheath as in the genus *Slavina*.

There are no eyes.

The prostomium is prolonged forwards as a long, narrow, cylindrical proboscis of varying length; it may be relatively very long—as much as 0.77 mm., or about six times the average diameter of the worm; in other specimens it measured 0.63 mm. (four and a half times the diameter of that particular specimen), or 0.33 mm. (nearly three times the diameter).

The ventral setæ are 5 to 8 or 9 per bundle; in segment ii they are 8 or 9; in iii and subsequent segments they are somewhat fewer—thus there may be 7 in iii, 5–7 in iv, 5–6 in v–ix; in the hinder part of the body there are often about 6, though as many as 8 seem not uncommon, in some individuals at least. The setæ are of the usual form, doubly pronged, the prongs being of equal thickness, but the distal rather longer than the proximal. There is no marked difference (as, for example, in some species of *Nais*) between the ventral setæ of the first few and those of more posterior segments; but the setæ of segment ii are longer than the others and the curve of the shaft less marked; the length of those in ii is about 107 μ , of those in iii about 90 μ , and further back about 71 μ . In segments ii and iii the nodulus is situated proximal to the middle of the shaft (proximal: distal :: 5:7); further back (e. g., in viii) it is practically at the middle (very slightly distal).

The dorsal setæ begin in segment iv; the bundles consist of hair-setæ only. The hairs are a single one per bundle, or sometimes two, in which case one may be long and one short. Three were seen occasionally, all of nearly equal length, or one considerably shorter than the other two; once four setæ were seen in a bundle. All are slightly bowed, and all are relatively stout—very noticeably so, compared with what is usual in worms of similar size. These hair-setæ increase in length for a few segments from the beginning; in one specimen in segment viii an enormous one was seen, 0.6 mm. in length, or nearly as long as the part of the body in front of it, and one of similar length in xi; in xii there were two notably long setæ. In a second specimen, while the most anterior hairs were only 0.16 mm. in length, those in viii were 0.46 mm., those in ix 0.56 mm.; behind this the length decreased, and in xiii the setæ measured 0.39 mm. In a third the length of those in xi was 0.5 mm., in xiv 0.4 mm. The longest that I measured was 0.63 mm.; the stoutest were 4 μ in diameter at the base, while others were of varying thickness down to 3 μ or rather

A fine serration is visible on the convex side of the hair-setæ in the distal half of their extent; the points of the serration are 12 μ apart near the middle of the setæ, but are closer together near the tip, at intervals of 8 μ or less.

The pharyngeal mass occupies segment ii and part of iii. The cesophagus is long, narrow, and straight. The stomach is situated in vii and viii, between the levels of the setæ of vii and of viii; or it may be definitely in viii: the body is slightly swollen about this region. Sections show that the epithelial cells of the stomach lining possess each an intracellular canal opening into the lumen; such canals, well known to occur in the Enchytræid genus *Fridericia*, have previously been described in certain species of *Pristina*.

Septal glands are present, as usual in the genus, in segments iv, v, and vi.

In one specimen which was sectioned the earliest stages of development of the sexual organs were seen; testes had formed in segment vii and ovaries in viii.

In the budding-zone seven of the newly-formed segments go to form the head of the posterior individual.

Pristina (as hitherto known) is one of the two genera of Naididae (the other, *Naidium*, being without a proboscis) in which the dorsal setæ begin regularly in segment ii, and in which, therefore, "cephalization"—the specialization of the anterior region to form a head—is confined to the first segment. In the remaining genera of the family the dorsal setæ (when present) begin as a rule, though not invariably, in segment vi; and the present species thus seems, at first sight, to occupy an isolated position in the family, such as might entitle it to constitute an independent genus.

But it is to be remembered that variation in the degree of cephalization is already known in a few genera. Thus, in *Aulophorus* the dorsal setæ begin in some species in vi, in some in v, in one in iv; in *Branchiodrilus* very various degrees of cephalization are found, the dorsal setæ beginning in ii in *B. senperi*, in vi in *B. hortensis*, and in any intermediate segment in *B. menoni*. In *Nais* (*Naidium*?) *dadayi* also the degree of cephalization varies even within the species.

The present specimens show the other characteristics of *Pristina*—those peculiar to that genus and those which it has in common with *Naidium*:—the proboscis, the septal glands, the intracellular canals of the stomach epithelium, the formation of seven (instead of five) new anterior segments in the budding-zone, and the position of the gonads in segments vii and viii (instead of v and vi). It seems, therefore, advisable to include them as representatives of a somewhat aberrant species of *Pristina*.

Genus *NAIS* Müll., em. Vejd.

NAIS PARAGUAYENSIS Mich.

1921. Swamp at Makthlawaiya. 6. vi. 27. Two specimens, neither sexual.

I subjoin a few notes on the present specimens, though the species is already fairly well known.

Length 14–23 mm.; maximum diameter 0.58 mm. In the shorter specimen the hinder end was injured; in the other there were 144 segments with setæ, behind which 10 more annulations were distinguishable, and finally a region in which segments were not differentiated at all. No budding-zone was present.

The dorsal setal bundles consist of a single hair with a single needle ; sometimes there is a short second hair ; once two needles were seen. The hairs are equal in length to the diameter of the body ; if there is a second short hair it is only half the length of the first, or even less.

The dorsal needles have the form illustrated by Michaelsen ('05 a) and myself ('09) ; in length they are up to 192μ in length and as much as 7μ in thickness ; but their size varies—they may be 172μ , 147μ , or as little as 124μ in length, and correspondingly thinner.

The ventral setæ are 3 or 4 per bundle, occasionally 5, regularly 3 towards the hinder end. The prongs are equal in length (in the segments behind the most anterior, at least), the inner (proximal) twice as thick at its base as the outer (distal). Michaelsen describes a slight difference between the setæ of the anterior segments (ii-v) and those behind ; in the former the outer prong is a little longer than the inner and its equal in thickness, while in the middle of the body the outer prong is of equal length with the inner, but is somewhat slenderer. I should not have noticed any such difference in the present specimens if I had not, noting Michaelsen's statement, specially examined for it : *possibly* there is some difference similar to that described by Michaelsen, but it is difficult with such a paucity of material, and that preserved, to be certain of such minute details. The length of the ventral setæ in the anterior segments (ii-v) is 123μ , and the nodulus is distal to the middle of the shaft (distal : proximal :: 13 : 17) ; the length and proportions are the same in segment vi.

It is rather remarkable that there should be such a marked difference in size between the present specimens (the one which is complete being 23 mm. in length) and those obtained in Paraguay by Daday and examined by Michaelsen (3-5 mm.) : but, given the difference in size, the difference in the length of the dorsal needles (up to 190μ as against 60μ) is not extraordinary. The number of seta-bearing segments (144 as against 30-48) is also much greater in the present examples.

Nais paraguayensis has also been found in several places in India. The Indian worms are, like the present specimens, larger and possess many more segments than the original examples studied by Michaelsen. In India the species has given rise to two varieties.

A budding-zone has never been observed in this worm ; I suggested ('21) that it probably multiplied by simple fragmentation and production of new segments (to form the tail and head respectively of the resulting individuals) after division, instead of before division as in the usual condition. Aiyer ('24) has since shown this supposition to be correct.

NAIS PECTINATA Steph.

278. Mud in pond in pasture, Makthlawaiya. 5. xi. 26. Several specimens, none sexual.

Since this species has hitherto been known only from India, I give a few details of the present specimens for the purpose of comparison.

Length 2.5–3 mm. : diameter 0.16 mm. Segments 22–31, sometimes with a short undifferentiated region behind the last countable segment. No budding-zone seen in any of the specimens.

The dorsal setal bundles consist regularly of one hair and one needle. The hairs are in length equal to the diameter of the body—about 0.16 mm., or sometimes rather more, probably nearly 0.2 mm. if the part of the seta within the body is included. The needles are slightly sickle-shaped, 53μ in length : their tips are pectinate (Pl. 17, fig. 1), the inner prong being the thickest and longest, the outer rather shorter and thinner, the two intermediate prongs a little shorter still and very fine indeed : the two larger prongs can be distinguished with the ordinary high power, the intermediates only with the oil-immersion.

The ventral setæ in the greater part of the body (behind segment v) are usually three per bundle : once four were observed, and towards the hinder end the number falls to two. In length they are $53\text{--}60\mu$: the terminal prongs are equal in length, while the inner is twice as thick at the base as the outer. In the anterior segments (in v) they are three per bundle, and are slenderer than in the more posterior segments, but of the same length : the outer prong is rather longer than the inner, and is more nearly its equal in thickness than in the remainder of the body.

There are differences, not altogether slight, in the shape, proportions, and numbers of the prongs of the dorsal needles between the present specimens and those originally described by me in India (Stephenson, '10) which can best be appreciated by a comparison of Pl. 17, fig. 1 with that in the paper just referred to. In some ways the conformation of the needles in the present specimens approaches that in the var. *inæqualis* (Stephenson, '11), which, like them, has two slender intermediate prongs, but in which the outer prong is very much smaller than the inner. The var. *inæqualis*, however, is often much larger, with a larger number of segments and a larger number of ventral setæ per bundle.

Genus AULOPHORUS Schmarda.

AULOPHORUS CARTERI, sp. n.

162. In tubes formed of the spores of the water-ferns *Azolla* and *Salvinia*; climbing on vegetation on the surface of the swamp, Makthlawaiya, 30. ix, 26. Several specimens, none sexual.

163. Makthlawaiya. 29. ix, 26. Several specimens, none sexual.

The worms were partly within and partly projecting from tubes, the projecting portion being the hinder end. The tubes are quite straight, 4–6 mm. long, 0.6 mm. in diameter, dark in colour, and made up for the most part of a large number of small spherical pellets fitted together in a single layer. The individual pellets are ca. 0.2 mm. in diameter, and were identified by the collectors as the spores of the ferns *Azolla* and *Salvinia* ; mixed with them are occasionally to be seen other objects—a Polyzoan statoblast (twice), a few

irregular masses (somewhat larger than the spores) of vegetable tissue, and a diamond-shaped structure with much rounded angles, apparently somewhat like the spores in structure, which I did not identify.

The length of the single animal (one without a zone of fission) is 2 mm.; chains are 4–5 mm. in length. In diameter the worms are 0.14–0.21 mm. The single animal may consist of 22 segments, with, in addition, an undifferentiated region in which distinct segments are not yet visible. In a worm which shows a fission-zone the anterior component has 17 or 18 segments ($n=17$ or 18), and the posterior component 12, 14, 16, or 17 segments, again with a terminal undifferentiated region. Of the new segments produced in the budding-zone the last five form the head of the hinder animal.

The prostomium has the form of a blunt and rounded equilateral triangle. There are no eyes.

The ventral setæ—double-pronged crotchets, as usual—are perhaps most often 5 per bundle; in the anterior segments the numbers are 5–7, further back 5–6, and lastly 3–4 per bundle. They are divisible into two groups, those of segments ii–v and those of the remaining segments (Pl. 17. fig. 2). Throughout the greater part of the body (the second group) both prongs are short, and the inner of the two is very stout—several times as thick as the outer—and distinctly the longer of the two; in length the setæ are 64–72 μ . In segments ii–v the ventral setæ are much longer—up to nearly 120 μ , but of the same thickness (2.5 μ), as the posterior setæ; both prongs are relatively long, the outer of the two, however, considerably longer and a little thinner than the inner. I was unable to ascertain the position of the nodulus in the two groups.

The dorsal setæ begin in segment vi; in the middle of the body the bundles are often composed of two hair-setæ and two needles, or two hairs and one needle, sometimes of one hair and one needle, once of two needles and one hair. Bundles of one hair and one needle are common towards the hinder end. The hairs are straight, without serration; in length they are about equal to the diameter of the body, or are often less—or, at any rate, project from the body for a distance which is less than the diameter of the worm.

The needles (Pl. 17. fig. 3) are 82–100 μ in length, almost straight, rather stout, and project considerably from the surface; the distal end is bifurcated, and between the two prongs stretches a transparent web; I could not distinguish any ribbing on the web. One prong is often much stronger than the other (Pl. 17. fig. 3, c). The prongs diverge at their tips to a span of 7 μ or 9 μ .

The body terminates behind in a branchial fossa from the hinder and lower border of which project the two palps which are characteristic of the genus; these measure 0.14–0.21 mm. in length. But the curious thing is that the gills are never visible in the fixed specimens. It is usual, of course, in this genus and in the related *Dero* to find the gills contracted in the preserved worms—often to such a degree that they are countable only with difficulty; and Bousfield ('87), in his revision of the genus *Dero* (which then included *Aulophorus*), has called particular attention to the danger of attempting to identify or describe spirit material, and to the enormous difference between the fully

expanded living and the contracted preserved specimens. But even so, the gills in the present specimens are extraordinarily obscure.

In addition to this absence of visible gills the worms show another peculiarity : the hinder end appears to be cut off vertically, so that the branchial fossa looks directly backwards, instead of, as usual, backwards and upwards.

The exact condition of the hinder end and gills could only be elucidated by sections. Of four specimens sectioned, the first was found to be so shrivelled as to be incapable of interpretation ; in the second there were no distinct gills, but a slight projection was present on one side of the fossa, not on the other : the third series is equivocal,—if there are any gills, they are confined to a single section 6 or 7 μ thick—but the structures in question do not really look like gills, and seem to be irregular projections of the wall of the fossa, mainly on one side. The fourth series is the best ; here, on each side of the hinder part of the floor of the branchial fossa, there is a short ridge which projects backwards freely for a short distance between the palps, i. e., a single pair of short gills.

In this species, therefore, while the non-retractile and non-vascular palps are well developed the gills seem to be regressing ; they are apparently variable in the degree of their development, and are at most one small pair.

AULOPHORUS BORELLI (Mich.).

161. Makthlawaya. 29 ix. 26. A number of specimens, none sexual.

277 Makthlawaya. 4. xi. 26. A few specimens (along with *Aulophorus pectinatus*), none sexual.

In the year 1900 Cognetti ('00) described from the marshes of Carandasinho in Matto Grosso (Brazil), on the left bank of the Paraguay River, 60 km. N.E. of Corumbá, from the collection made by Borelli, a single example of a worm which lacked the anterior extremity. He did not affix to the description a specific name ; but Michaelsen ('00), considering that the features described were sufficiently characteristic, called it *Dero borelli*. The present specimens seem to belong to this species : and I am thus, fortunately, able to complete the account of the worm, of which only the posterior end has hitherto been known.

The specimens vary in length : the average is about 20 mm., but the longest is 35 mm. ; in diameter they are 0.44 mm. The longest worm had 147 well-formed segments, succeeded by a terminal region of apparently very recent production in which about 17 pairs of very young setal bundles were distinguishable ; but a much shorter worm—one about 16 mm. long—had 154 segments.

No budding-zone was seen.

The prostomium is rounded. There are no eyes.

The dorsal setæ begin in segment v : each bundle consists of a single hair and a single bifid needle-seta (occasionally in the anterior part of the body two needles). The hair-seta is in length less than the diameter of the body. The needle-setæ (Pl. 17. fig. 4) are 120 μ long, somewhat sickle-shaped, and bifid at the tip ; the inner prong is equal to the outer in length, but is twice as thick at the base ; a slight thickening, representing the nodulus, is situated at the

junction of the distal curved and proximal straight portions, one-third of the length from the tip.

The ventral setæ are commonly 4, but occasionally 5 per bundle in the anterior segments; behind this they are 3 per bundle for a long space, diminishing to 2 at the hinder end; in one specimen the bundles contained only 2 setæ each over a long distance in the hinder region. The setæ are of the usual sigmoid form and double-pronged; those of all segments behind the first few are $125\ \mu$ in length or less, with the nodulus distal (two-fifths of the length of the shaft from the tip) and the prongs equal in length, but the inner very much thicker than the outer—three times as thick or nearly so. Those of the most anterior segments are about $148\ \mu$ in length; the shaft is less curved, and the nodulus, though still distal, is nearer to the middle of the shaft—at three-sevenths or four-ninths of its length from the tip; the relations of the prongs are not very different from those of posterior segments, but both prongs are relatively a little longer and the outer is slightly longer than the inner.

In the bundles which consist of only two setæ one seta is considerably shorter than the other—*e. g.*, $100\ \mu$ as against $120\ \mu$,—and has somewhat more pronounced curves. Sometimes in the bundles of three setæ I have detected the same relations as to length, thickness, and curvature as in *A. pectinatus* (v. inf.); but in other bundles of three setæ this is scarcely to be made out.

The hinder end is expanded to form an approximately circular branchial fossa. The palps, projecting backwards from its hinder margin, are 0.26 mm. long in the preserved worms. The gills are four pairs of radiating ridges on the floor of the fossa, the dorsal (or most anterior) pair being usually smaller—it may be considerably smaller—than the rest. In one specimen a small additional more dorsal gill was present on one side.

The œsophagus broadens gradually to form the intestine, which may be said to begin about segment x; there is no stomach.

Asexual reproduction must take place by fragmentation and subsequent production of new segments to complete the tail and head ends of the anterior and posterior worms respectively. This is to be concluded, not so much from the fact that I never saw a zone of budding in any of the specimens, as from the form of the anterior end of one of them. In this worm the first four segments form a narrow projection slightly more than half as thick as the body behind them; they thus appear to have been produced in the way of regeneration after separation, since, if they had been produced in a budding-zone, they would have been approximately of the same diameter as the rest of the worm. The number of new segments which go to form the head of the worm is thus four, which corresponds to the fact that the dorsal setæ in this species begin in segment v.

AULOPHORUS BEADLEI, sp. n.

1276. Swamp at Makthlawaiya. 9. v. 27. Several specimens, none sexual.

Length 4 mm.; diameter 0.25 mm. Segments 26–44, sometimes with a

shorter posterior region in which segments are not yet differentiated. All the specimens were single individuals; a budding-zone was not seen in any. Here, again, it appears that fission takes place by simple fragmentation, not by the formation of a budding-zone. In one specimen the region in front of the first dorsal setæ (in segment vi) was very short (from tip of prostomium to the dorsal setæ of segment vi measured 0.22 mm., i. e., the whole length of the cephalized region was less than the diameter of the body), though in it a cerebral ganglion was seen and possibly also the beginnings of the ventral setal bundles: this animal had obviously been recently detached, and the head was still in a very immature state: in other words, the head is formed after detachment, and not before (not in a budding-zone). In the more usual condition the segments of the head are completely formed and their setæ fully developed before separation.

From an examination of the newly formed hinder ends of some of these specimens it appears that $n=19-26$.

One specimen is enclosed in a delicate structureless and transparent tube, equal in length to the body of the animal, and in diameter 0.44 to 0.53 mm.; the palps at the hinder end of the worm just reach to one end of the tube, the head protrudes slightly from the other.

The head is somewhat bulbous, is thicker than the rest of the body, and is relatively short even when fully formed. The prostomium is very blunt and short. There are no eyes.

The dorsal setæ begin in segment vi: each bundle consists of one needle and one hair-seta. The hair is shorter than the diameter of the body. The needle-seta (Pl. 17. fig. 5), 75μ in length, is slightly sickle-shaped, the distal curved portion being one-third of the length of the seta; the tip is finely forked, and with the oil-immersion lens there appears to me a slight irregularity within the notch of the fork.

The ventral setæ are commonly 5 per bundle; in some of the anterior segments there may be 6, and towards the hinder end 4 is not an uncommon number. There is a difference between the setæ of the cephalized segments and those of the rest of the body. The setæ of the greater part of the body are 80μ in length; the nodulus is situated distal to the middle of the shaft (distal: proximal:: 7:9); the outer prong is slightly longer than the inner, while the inner is half as thick again at the base as the outer; the shaft, by comparison with the setæ of many other forms, is not very strongly curved. The setæ of the anterior group are 140μ long; the nodulus is proximally situated on the shaft (distal: proximal:: 4:3); the prongs are longer than in the posterior group, the outer prong being longer than the inner, while both are equal in thickness.

The palps are 0.26 mm. in length, 33μ in diameter near their base; in most specimens the palps are bent forwards, mixed up with and almost indistinguishable from the gills. The gills are four pairs, and appear as ridges on the wall of the branchial fossa.

There is no stomach. The chloragogen cells begin in segment vi.

AULOPHORUS PECTINATUS, sp. n.

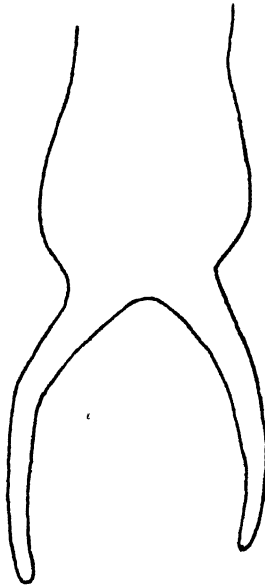
277. Makthlawaiya. 4. xi. 26. Several specimens, none sexual.

Length 12–16 mm. ; diameter 0.3–0.35 mm. In one specimen 108 segments were counted, of which the last 25 or more were short, small, and obviously newly formed ; in another, with 113 segments, about 28 were similarly newly formed. It is possible, therefore, that fragmentation takes place between the 80th and 90th segments ($n=80-90$).

The prostomium is triangular and bluntly pointed. There are no eyes.

The dorsal setæ begin in segment v, the bundles consisting of one hair- and one needle-seta. The hair is $280\ \mu$ long, including the basal portion within the

TEXT-FIG. 1.



Aulophorus pectinatus, hinder end in outline, to show the form of the palps.

body—i. e., is less than the diameter of the body. The needle (Pl. 17. fig. 6) is slightly sickle-shaped, in length $102\ \mu$, the bend at the junction of straight and curved portions being $30\ \mu$ from the tip ; there is no swelling (representing the nodulus) at the bend. The tip is forked, but the forking is less obvious than in *A. borellii* ; between the main prongs of the fork are two, three, or occasionally four fine intermediate prongs, only seen under the oil-immersion lens.

The ventral setæ in the anterior part of the body are 3 and often 4 per bundle, in the posterior part regularly 3, or towards the hinder end 2 ; the prongs are of equal length, or the inner may be slightly longer ; the inner prong is twice, or even three times, as thick as the outer. In these bundles of three setæ there is a regular gradation in the characters of the individual setæ from the inner of

the bundle to the outer, the inner seta being longer, slenderer, less strongly curved, with nodulus more proximally situated, the outer shorter, thicker, more strongly curved, with nodulus more distally situated. Thus the innermost seta may be 140 or 127 μ long, the middle seta 131 μ , the outermost 119 μ or 106 μ ; in the innermost seta the nodulus may be almost at the middle of the shaft (distal : proximal :: 15 : 16), though it may also be much less (13 : 21); while in the outermost the proportions are represented by the ratios 2 : 3 or 11 : 18. I cannot say whether or not there is any difference between the setæ of the most anterior segments and those of the rest of the body.

The palps are 0.35 mm. long, in form slightly tapering, diverging at their bases, and then curving slightly towards each other (text-fig. 1). The gills are four pairs.

There is no stomach.

Family TUBIFICIDÆ.

Genus LIMNODRILUS Clap.

LIMNODRILUS CHACOENSIS, sp. n.

243. Rio Verde salt-ponds; mud of saline pools, salinity 1014.8; 15 miles N.W. of Makthlawaiya. 16. x. 26. Several specimens, some sexual.

256. Rio Verde salt-pools. 22. x. 26. Several specimens, some sexual.

1150. Rio Verde Riacho, 5 miles N. of Makthlawaiya; in mud of river-bed, water fresh 19. iv. 27. Several specimens, some sexual.

Length 10-20 mm.; diameter of anterior end 0.44 mm.; the hinder half of the worm is much thinner—0.18 to 0.26 mm. Segments 62-93, with sometimes a relatively long undifferentiated terminal region; in some specimens the posterior portion is moniliform, as if this region were going to break up by autotomy into single segments.

Prostomium small—one might almost say minute, triangular, and pointed.

The setæ begin in segment ii, and are all sigmoid double-pronged crotchets. As a rule in the most anterior segments there are 5 setæ per bundle, both dorsally and ventrally; in some of the bundles of the clitellar segments there are 6, in the middle of the body 4, and towards the hinder end 3 or even 2; the maximum number I observed in a bundle was 7.

The setæ are similar in characters, as in numbers, in dorsal and ventral bundles; in length they are 90 μ , with the nodulus slightly distal to the middle of the shaft and the two prongs equal in length, but the inner twice as thick at the base as the outer. Ordinarily the setæ project very little from the surface of the body; in some specimens they appear, probably owing to the contraction of the setal muscles, to be set on or in papillæ which may show prominently along the sides of the specimen.

The clitellum embraces segments xi-xii together with the hinder part of x (the portion posterior to the level of the setæ).

Some of the specimens appear to be abnormal in the structure of the alimentary wall. Thus in one of the sectioned specimens the lumen of the gut was much

swollen in the genital segments, so much so that the whole animal was distended in this region. The epithelium of the anterior part of the intestine was in this specimen of irregular height, in some places flattened and thin, and nearly throughout the swollen portion much lower than normal; the vascular sinus in the alimentary wall was very prominent.

The anterior part of the intestine may be filled out with a granular amorphous lightly or moderately deeply staining mass, as, for example, in the swollen region described above.

In some specimens (tube 243) the peritoneal covering of the gut is enormously swollen, and fills out the whole of the space between gut on the one hand and body-wall and septa on the other. The peritoneal cells are much elongated; apparently they are still a single layer, so that each cell stretches from gut-wall to parietes; they are clear, with sparsely granular contents. The worms of tube 1150 were not thus affected.

The condition in these worms reminded me of what I found in certain specimens of *Lumbricillus ægialites*, an Enchytraeid from Spitsbergen (Stephenson, '26); I am uncertain what the cause may be.

There is one pair of hearts in segment viii. A system of "cutaneous" or parietal vessels exists in the hinder part of the body; there are two (or ? more) vascular arches on each side per segment, regular in position, lying underneath (not contained within) the body-wall, on the parietal peritoneum.

The testes are in segment x, into which the male cells are shed; some developing sperm-morulae may be seen free in the segment.

The seminal vesicles are two, an anterior in segment ix (an anterior evagination of septum 9/10) and a posterior (a posterior evagination of septum 10/11); the latter, contained within the ovisac (a backward evagination of 11/12), extends back through more than one segment, as far as xiii.

The male funnels occupy their normal position in segment x, on the anterior face of septum 10/11. The vasa deferentia are long, relatively thick, much coiled tubes in segment xi, extending back into xii; in diameter they are about 30μ . The walls vary in thickness; in one region they are thin, 5 to 6μ , and the lumen is consequently wide; in other places the walls are thicker, 8 to 10μ ; or, again, the walls may be remarkably thick, so that the lumen is much reduced and becomes quite narrow. The tube is heavily ciliated internally; the nuclei of the wall are small, and if cut tangentially are seen to be elongated transversely to the axis of the tube. The vasa deferentia end by joining the atrium, not at its dorsal pole, but some little distance below this.

The atrium has a vertical position in segment xi; it is a wide tube which may be somewhat bent on itself; its length is $250-300\mu$, its diameter 90μ , or, in an advanced sexual stage, 120μ , and the thickness of its wall, which possesses a strong muscular layer, $16-25\mu$. The inner zone of the lining epithelium (*i. e.*, the part of the cells which is towards the cavity) stains a deep blue with Delafield's hæmatoxylin.

The prostate is fairly bulky, lobulated, solid, a mass of cells in segment xi

which surrounds part of the male deferent apparatus and joins the atrium near its upper end by a neck which is also solid; the cells constituting the neck penetrate the wall of the atrium and reach the lumen (as described, for example, by Mehra ('25) in *Tubifex*), causing a projection into the cavity. The cells of the prostate break down at sexual maturity, and coalesce to form an amorphous mass.

There is a short penis, very similar to that of *Tubifex* and unlike that of the common European species of *Limnodrilus*. The penis, when retracted within the body-wall, is contained in a penial chamber, the cavity of which opens on a moderately prominent papilla on the ventral surface of segment xi. In this condition the wall of the penis may show a reduplication, as figured, for example, for *Tubifex* by Miss Dixon ('15) or for *Limnodrilus virulentus* by Pointner ('11). The surface of the penis, as also the wall of the penial chamber, is covered by a layer of cuticle continuous with that of the surface of the body; this layer is somewhat strengthened over the penis, the reduplication, and the wall of the chamber; but there is no special thickening and no semblance of a rigid chitinous tube like that we are familiar with in most species of the genus.

No penial setæ were seen.

The ovaries are in segment xi. The ovisac, a backward evagination of septum 11/12, surrounds the sperm-sac (seminal vesicle), and, like this, extends backwards into segment xiii.

The spermathecae occupy segment x and open on the surface in the hinder part of the segment. In their early stages they are both confined within this segment, but at their full development they are, apparently, too large to be both accommodated in the same segment, and one may be seen turned backwards, its greater part lying in segment xi. The ampulla is a large and thin-walled sac, with, in its young stage, a shortly columnar epithelium; at maturity the ampullar epithelium degenerates. The duct, the narrow ectal portion of the apparatus, is sharply marked off from the ampulla at sexual maturity, and contains spermatozoa in an irregular mass (not in a spermatophore).

The cavity of the ampulla, however, contains a number of spermatophores—pear-shaped structures, with a much elongated narrow end. In length the spermatophores measure 400μ or perhaps more; the broad end is $50\text{--}56\mu$ in diameter and about 120μ in length, the extremely long "stalk" is about 20μ in diameter, and is several times as long as the broader end. The interior is hollow, and contains a darkly staining mass in both the broad and narrow regions; this is composed of the aggregated heads of the spermatozoa—i. e., the spermatophore is a case, a structureless wall, which encloses the spermatozoa with their deeply staining heads as a core. When the spermatophores in the ampulla of the spermatheca are few, the cavity of the organ is mainly occupied by an amorphous mass.

The worm just described differs markedly from most species of *Limnodrilus*, and resembles the genus *Tubifex* in having no long, rigid, chitinous penis-tube,

but a small copulatory organ covered with a scarcely thickened layer of cuticle ; the setal characters, however, distinguish it sharply from *Tubifex*.

Other authors, and in particular Michaelsen, have described forms with a penis similar to that of the present species ; and Michaelsen has shown ('14) that a series of intermediate conditions links this form of penis with that of the more familiar species of the genus. The rigid chitinous penis-sheath is therefore no longer to be looked on as an invariable characteristic of *Limnodrilus*.

The forms which resemble the present one in being without the rigid penistube are European or Asiatic in distribution. They are all distinct from *L. chacoensis*; thus, *L. virulentus* has only a very small prostate, and the proportions of the penis and of the parts of the spermathecal apparatus are different from those in the present form : *L. arenarius* has genital setæ in segment x, a single seta per bundle, and the spermathecae are confined to the anterior half of segment x ; *L. dybowskii* has, as a rule, not more than two setæ per bundle, and the penis and its sac are clothed with a very thick cuticle ; in *L. baicalensis* there are genital setæ in segment x, single in each bundle, and single-pointed ; in *L. heterochaetus* there are single-pointed setæ in the middle and hinder regions of the body, and the vas deferens is short ; *L. newaensis* has a longer penis than the present species, with a stronger thickening, definitely limited above and below, of the chitinous investment—a special chitinous ring, as long as broad, and there is only a single seminal vesicle—the posterior one.

Family MEGASCOLECIDÆ.

Subfamily OCNERODRILINÆ

Genus *KERRIA* Bedd.

KERRIA LIMOSA, sp. n.

164. Makthlawaiya ; from mud of shallow pools after rain. 30. ix. 26. Several specimens, some with sexual organs.

External Characters.

Length 20–28 mm. ; diameter 0·7 mm. Segments 95–127.

Prostomium almost tanylobous (?).

Setæ sigmoid, single-pointed, closely paired throughout the body ; $aa=2bc$ in the anterior segments, and further back this ratio may still be observed in some segments ; mostly, however, aa is relatively smaller, though still greater than bc . The dorsal bundles (cd) are situated in the lateral line (in the anterior part of the body at least), and dd is thus nearly equal to half the circumference.

The clitellum is not very easy to distinguish, even in sections ; it seems to include xiii or $\frac{1}{2}$ xiii–xx, $7\frac{1}{2}$ or 8 segments.

The prostatic pores are immediately outside seta b on segments xvii and xix, on round papillæ ; the papillæ of the same side are separated by a space about equal to the diameter of a papilla. One or other of the ventral setæ, a or b , is often (but not always) wanting in segments xvii and xix, and b may be absent in xviii also.

The openings of the vasa deferentia are not visible externally ; from sections, they are found to be on xviii, midway between the prostatic pores of the same side. Seminal grooves could not be distinguished.

The spermathecal pores are in furrows 7/8 and 8/9, approximately midway between the lines of setæ *b* and *c*.

Internal Anatomy.

Septa 5/6–8/9 are somewhat strengthened.

The pharyngeal gland-cells ("chromophil cells") extend backwards to segment vii. There is a gizzard in vii ; the muscular coat of the œsophagus is considerably thickened, but the diameter of the whole tube is not very greatly increased.

The calciferous glands or œsophageal sacs are present in segment ix ; they take origin from the œsophagus in the hinder part of the segment, and extend forwards. Their lumen is small, narrow and rather slit-like, and the very thick wall is honeycombed by a large number of blood-spaces, circular in transverse section, separated by a system of stout trabeculæ. Near the hinder end of the organ the blood-spaces join together, and so become fewer and larger. The structure is thus similar to that of the sacs of *K. pascuorum* (v. inf.).

The last hearts are in segment xi.

Testes and funnels are free in segment x ; in this segment are also a few sperm-morulæ. There are small seminal vesicles in ix and xi. The vasa deferentia end on segment xviii somewhat to the outer side of seta *b*, which is present in the sections.

The prostates (two pairs) discharge to the exterior on considerable cushion-like thickenings of the body-wall. The prostatic duct is muscular, of about the same diameter as the glandular portion of the organ ; its length (calculated somewhat roughly from the sections) is about $200\ \mu$; its lumen is very narrow throughout, and is not widened as it passes to the surface through the thickened cushions ; there is no copulatory sac. The glandular portion changes its characters gradually as it passes into the duct.

There are no penial setæ, the setæ of the ventral bundles near the male and prostatic pores not being modified in form.

The spermathecæ (Pl. 17. fig. 7) are two pairs, lying in segments viii and ix, and opening in furrows 7/8 and 8/9. The ental portion of the organ is tubular and twisted, its lumen narrow, not more than $6\text{--}8\ \mu$ in diameter, and sometimes apparently less ; a wider portion succeeds, sharply marked off from the foregoing, its cavity somewhat irregular, $20\text{--}28\ \mu$ in transverse diameter ; and this is followed by the duct, which is short and immediately enters the body-wall, where it is surrounded by an extraordinarily thick muscular coat of its own. The whole diameter of the spermatheca, including the thickness of the walls, is $34\ \mu$ in its ental tubular portion and $70\ \mu$ in its ectal more swollen part.

Remarks.

The specimens were too small (less than three-quarters of a millimetre in

diameter) to dissect or to make much out by external examination, and this must excuse the shortness of the above account; but the species appears to be sufficiently characterized by the features given. *K. subandina* (Brazil and the Argentine) is, perhaps, its nearest relative; but the setal relations (*aa* somewhat less than *bc* in *K. subandina*) and the shape of the spermathecae (the ampulla elongatedly ovoid or pear-shaped in *K. subandina*) will easily distinguish the two. The spermathecae are somewhat reminiscent of Rosa's figure of the organ in *K. garmani* (Rosa, '95); but here again the setal relations (*aa* less than *bc* in *K. garmani*) are distinctive.

KERRIA HORTENSIS, sp. n.

561. Garden at station, Makthlawaiya. 7. xii. 26. two small specimens, sexual.

829. Same locality. 2. ii. 27. Several specimens, some sexual. (Said not to have been known before the ground was cultivated.)

External Characters.

Length 35–48 mm.; diameter 1–1.5 mm. Segments 86–91.

It is difficult to see the conformation of the prostomium; sometimes it seemed zygolobous, sometimes prolobous; but I think it is really slightly

TEXT-FIG. 2.



Kerria hortensis, outline of prostomium.

epilobous, a pair of short grooves being directed inwards and slightly backwards from the lateral margins at the base (text-fig. 2).

The setae are closely paired; in the middle of the body *aa* is approximately equal to *bc*, but is slightly greater than *bc* behind the middle, and distinctly so ($=1\frac{1}{2} bc$) in front of the clitellum; *dd* is equal to half the circumference in the anterior part of the body (in front of the clitellum), but behind the middle of the body is less than half the circumference.

The clitellum includes segments xiii–xx ($=8$); it is saddle-shaped.

The prostatic pores are two pairs, on xvii and xix, each situated on a relatively large and prominent papilla. The papillae of each side join each other in such a way that only a transverse groove intervenes between them; or one might say that the two apertures of the same side are situated on the widest and most prominent parts of a dumbbell-shaped eminence which is divided across its middle by a furrow. The prostatic pores of the same side are united by a longitudinal seminal groove, with a straight course, which crosses the transverse groove between the two papillae, the two grooves together having thus a cruciate appearance. The pores and grooves are wide apart—about $\frac{1}{2}$ of the circumference; they are thus below the line of the lateral setae, but nearer the line of

c than *b* ; on looking down on the worm from above the eminences on which the pores are situated stand out noticeably at the sides.

The male pores (endings of the vasa deferentia) are apparently where the two grooves (mentioned above) cross ; here there seems to be a slight pitting.

The spermathecal apertures are not visible on the surface, but the organs can be seen through the body-wall ; they lie well above the lateral line of the body, and, as determined by sections and dissection, the apertures are in furrows 7/8 and 8/9, in the dorsal quadrants, about one-third of the circumference (measured over the dorsum) apart.

Internal Anatomy.

Septa 6/7, 7/8, and 8/9 are somewhat thickened.

The œsophageal wall is slightly strengthened in segment vii, so that we may speak of a rudimentary gizzard in this segment.

A pair of œsophageal sacs are present in segment ix : these arise ventrolaterally from the œsophagus in the hinder part of the segment, and extend forwards to near its anterior limit ; they are rather wider in front than behind. Transverse sections (Pl. 18. fig. 9) show that the sacs have a very simple structure : projecting into the interior are 20–25 low lamelliform ridges, longitudinally disposed, of different heights, some higher some lower.

The last hearts are in segment xi.

The testes and male funnels are each a single pair, free in segment x. A pair of small seminal vesicles are present in segment xi ; none were seen in ix in the specimen which was dissected, but a pair of small vesicles were discovered in this segment in the example which was sectioned.

The prostates are two pairs ; each is an elongated tube, extending backwards in a somewhat twisted course through several segments, to xxii or xxiv. The duct is the short terminal portion of the organ, about 1 mm. in length ; it is very narrow—much narrower than the glandular part ; the one portion passes suddenly into the other.

No penial setæ were observed.

The spermathecæ are two pairs, in segments viii and ix ; they are tubular in form (Pl. 17. fig. 8), the ental portion being somewhat, but not much, wider than the rest ; there is no sharp distinction between one part and another. A short terminal portion, however, which may be called the duct, is distinctly narrower, though even here there is no sudden change, and one part passes gradually into the other. The duct is about one-fifth of the length of the ampulla ; there is no diverticulum or swelling on the duct.

The spermatheca appears always to be bent on itself, sometimes more than once (*cf.* Pl. 17. fig. 8 *b*). The epithelium of the sac is columnar, of irregular height.

Remarks.

The species is distinguished from all others of the genus by the dorsal position of the spermathecal apertures.

KERRIA PASCUORUM, sp. n.

315. Mud of ponds in pasture, Makthlawaiya. 9. xi. 26. Seven specimens, four with sexual marks.

External Characters.

The length of the longest specimen is 60 mm. ; other specimens measured 33, 42, and 52 mm. The maximum diameter is 0.8 mm. The number of segments in the longest specimen is 144, in the shortest 110 ; but the latter specimen shows a number of very short segments at the hinder end, and is, perhaps, regenerating a lost tail. The colour is a nondescript greenish yellow.

The prostomium is small and probolous.

The setæ are closely paired : $aa = 3ab = bc$; $ab = cd$; dd is equal to half the circumference. The same ratios hold both in front of and behind the clitellum.

The clitellum appears to extend over xiv-xx (=7) ; but from the examination of sections it seems that the greater part of xiii is also to be included ; it is saddle-shaped.

The prostatic pores are on xvii and xix, on small porophores, which in turn are situated on moderately large and conspicuous papillæ. The papillæ are longitudinally oval in shape, twice as long as wide, and in length take up their proper segment with a little of segment xviii ; so that a small part of xviii is left unoccupied by and between the two papillæ of the same side. The interval between the two papillæ of the same segment, xvii or xix, is equal to the transverse diameter of a papilla. The papillæ overhang at their margins. The prostatic pores are one-third of the circumference apart, between the lines of the ventral and lateral setæ, but nearer to the line of b than to that of c . Sometimes the ventral surface is concave in this region (in the preserved specimens), so that the apertures face somewhat inwards towards each other. The seminal grooves are straight ; they appear in sections as deep trenches.

In one specimen the ventral surface of segment xviii was raised and "glandular" in appearance, so that the surface of segments xvii and xix by comparison appeared flat and somewhat depressed. In the transverse specimens of one of the specimens also this glandular pad was well marked.

The spermathecal apertures are determinable from sections as being situated immediately behind furrows 7/8 and 8/9, in line with the lateral setæ—perhaps more accurately in line with seta c .

Internal Anatomy.

Septa 5/6-8/9 are somewhat thickened, and are strongly conical backwards ; 9/10 and succeeding septa are thin.

The chromophil cells extend backwards into segment vi, with a few also in segment vii.

. There is a moderately developed gizzard in segment vii ; though the increase in the thickness of the muscular layer of the œsophageal wall comes out very well in sections, there is not much increase in the width of the tube as a whole.

The œsophageal sacs (Pl. 18. figs. 10*a*, 10*b*) in segment ix are given off from the alimentary tube in the hinder part of the segment; they extend forwards, and are attached to the anterior septum of the segment by a cord, really a blood-vessel. They are pear-shaped, with the broad end anterior. In transverse section they have the "honeycomb" appearance of those of *K. limosa*, with a small narrow slit-like or star-shaped central lumen, as described in the introductory section.

The last hearts are in segment xi.

Testes and funnels, with some male genital products, are free in segment x. Seminal vesicles are present in ix and xi, in the latter segment of moderate size, in both very deeply lobulated or actually racemose.

The prostates extend back through several segments: neither pair extends back behind segment xxii (in two series of sections), or, at any rate, they come to an end before segment xxiv (a third series). The diameter of gland and duct is much the same, but the wall is constituted mainly by the epithelium in the glandular portion, by the muscular layer in the duct. The gland-cells are essentially a single layer, columnar and much elongated, with some basal cells between their outer ends.

The duct is about, or a little more than, a segment in length: it has a very strong muscular coat throughout its extent as far as its entry into the body-wall. It penetrates the substance of the papillæ, already described, as a very fine tube, widening, however, close to its termination on the surface; but there is no copulatory pouch nor special muscular investment in this terminal part of its course.

The substance of the papilla consists of a dense tissue of interlacing muscular fibres and (?) connective-tissue cells; the circular muscular layer of the body-wall contributes to the muscular mass, and can be distinguished in transverse sections as a separate element traversing the substance of the papilla.

What may be called "nests" of fairly deeply staining cells, with 6 to 8 or more cells in a section of each nest, are seen in the mass of muscle of the papilla, deeply situated, within the circular muscular layer. In what appears to be a fairly early stage of their development they have no communication with the surface; but later on they form, taken together, a large somewhat lobulated mass, and some of the cells stain much more deeply, in consequence of what seems to be a mucoid change. These deeply staining cells, or their secretions, begin to push outwards, and slender processes of the deeply staining mucoid material pass between the other components of the papilla and are discharged on the surface. Later, some of the cell-masses lose their structure, the individual cells are not to be distinguished, the whole stains an intense blue (with Delafield's hæmatoxylin), and the mucoid secretion makes its way to the surface by a number of slender channels in the immediate neighbourhood of the prostatic pore. The mass of cells is in transverse section immediately to the outer side of the prostatic duct as it enters the body-wall.

The vas deferens ends in line with and midway between the two prostatic pores of the same side ; all three apertures may be cut in a single longitudinal section.

The spermathecæ are two pairs, in segments viii and ix ; the ampulla constitutes a sac of an elongated ovoid or cylindrical shape ; it may be bent on itself, and may show a constriction at the bend. The duct is short, and is embedded in a particularly massive muscular thickening ; thus the diameter of the organ as a whole does not diminish on passing from the ampulla to the duct, though the narrowing of the lumen as the duct is reached is considerable and fairly sudden. The wall of the ampulla consists of a single layer of epithelium, with indications of a thin peritoneal coat outside this, but no visible muscular layer.

Remarks.

The present species comes near *K. eiseniana* Rosa, from Asuncion and Rio Apa in Paraguay (Rosa, '95). It differs, however, in its smaller size (*K. eiseniana* is 2 mm. in diameter), in the setal ratios (*dd* being less than half the circumference in *K. eiseniana*), in the characters of the male field and papillæ, and in the length of the prostates (which extend back for a dozen segments in *K. eiseniana*) and their ducts (which are three to four segments long in Rosa's worm).

Family GLOSSOSCOLECIDÆ.

Subfamily GLOSSOSCOLECINÆ.

Genus OPISTHODRILUS Rosa.

OPISTHODRILUS BORELLII Rosa.

1182. Makthlawaiya, in streams flowing from higher ground into swamp after rain. 22. iv. 27. Several specimens, some sexual.

This species was originally described[†] by Rosa ('95) (Borelli's collection) from Resistencia (Chaco Argentino) and Luque (Central Paraguay). Michaelsen ('17) has since received specimens from N. Paraguay, and has supplemented Rosa's account. I add a few notes on certain features of the present specimens.

The longest examples measure 135 and 137 mm.—considerably more than Rosa's ; the number of segments is 177–221.

The setal intervals are thus :—in the middle of the body $aa = \frac{1}{2} bc$, and dd is about half the circumference ; on the clitellum $aa = \frac{1}{2} bc$, dd is rather greater than half the circumference ; in front of the clitellum, towards the anterior end of the animal, the relations are reversed— $aa = 1\frac{1}{2}$ to $1\frac{1}{2} bc$, while dd is about $\frac{2}{3}$ of the circumference.

The anterior limit of the clitellum is not well marked ; though it sometimes seems as if segment xiii and perhaps three-fifths of xii also were included, its full development appears to coincide with segment xiv ; posteriorly it includes the greater part of xxiv.

The ventral setæ of segment vi on one or both sides, the ventral setæ and sometimes the lateral setæ of vii, and those of ix and x even more markedly, are situated on round flattish papillæ, which in segments ix and x take up nearly the whole length of the segment. Only in one specimen, and then in only a slight degree, were such papillæ present at the site of the ventral setæ of viii. Similar papillæ are seen on segments xxx-xxxvii, and less markedly on xxix and xxxviii; in one specimen they extend forwards in series with the above, though only slightly marked, as far as xxv.

The "walls" or "ridges" of puberty extend on each side through segments xxxii-xxxvi, in one specimen encroaching on xxxi also. These are low, broad, and flat ridges, situated between the lines of setæ *b* and *c*, and taking up the greater part of the space between these lines. The flat surface of the ridge is marked by two longitudinal grooves, a little within the inner and outer margins respectively, which curve towards and meet each other at the hinder end. The more central portion of each ridge, within the longitudinal grooves, is of slightly different tint from the margins—rather darker in colour.

The vesiculæ seminales, of the curious form described by Rosa, extend back in the dissected specimen only to segment xvi on one, to xviii on the other side (in Rosa's specimens to about segment xxx).

Genus DIACHÆTA Benh.

DIACHÆTA EXUL, sp. n.

1182 (in the same tube as *Opisthodrilus borellii*). Makthlawaiya, in streams flowing from higher ground into swamp after rain. 22. iv. 27. Seven specimens, mostly sexual.

External Characters.

Length 48-70 mm.; maximum diameter (at clitellum), 3 mm. Segments 151-154; these are the numbers in the shortest and longest examples respectively, many segments of the former being extremely short. Colour a light brownish-green or olive.

Prostomium absent (or invisible).

Dorsal pores absent; but there are indications in furrows 10/11-13/14 of pores now obsolete and impervious; small dark spots in the places where the pores would be found if present indicate a divergence of the muscle-fibres at these points.

Setæ closely paired; throughout the body $aa = \frac{1}{2}bc$ (or occasionally $\frac{3}{4}bc$, or in front of clitellum nearly equal to bc); dd is about half the circumference, or it may be rather less on the clitellum. The close pairing of the setæ is maintained to the hinder end.

The nephridiopores are in the line of setæ *cd*, and are especially conspicuous on the clitellum.

The clitellum extends over segments xiv-xx (=7), and is ring-shaped; the setæ and intersegmental furrows are present and easily visible.

On segment xviii, just outside the lines of the ventral setæ and extending through the anterior half of the segment only, are a pair of crescentic or parenthesis-like grooves, the concavities turned towards the middle line (Pl. 18, fig. 11); they are placed slightly obliquely, with their anterior ends, at the level of furrow 17/18, a little closer together than the posterior. Surrounding these grooves is a well-marked ridge, which in turn is bounded by a narrow groove; the ridges extend in front slightly on to segment xvii. The whole has rather an ear-like appearance.

In one specimen, and slightly in another, the ridges with the included grooves are much contracted from side to side, hence narrower and more prominent; their ends are joined transversely across the ventral surface by narrow ridges, one along the posterior border of segment xvii and one along the posterior border of xviii, so that the ventral surface of xviii appears as a slightly sunk flat rectangular area.

The female apertures are inconspicuous; from dissection they are in the immediate neighbourhood of the ventral setæ of segment xiv, perhaps just to the outer side of *b*.

There are no spermathecal pores.

The ventral region of segment xi is whiter and more opaque in appearance than neighbouring segments; this is due to the contained male organs and genital products.

Internal Anatomy.

Septa 6/7–11/12 are strengthened, the majority moderately, the last one or two rather less than the others; these are all strongly funnel-shaped, the narrow ends of the funnels pointing backwards. Septa 12/13–13/14 are slightly thickened.

There is a well-developed gizzard in segment vi. The portion of the œsophagus in front of the gizzard is thin-walled and crop-like.

Calciferous glands are present as elongated sacs in segments vii, viii, and ix; each is finger-shaped and arises ventrally from the œsophagus by a narrow stalk, extends forward and upwards in the segment on the side of the œsophagus, and ends by tapering to a point at its free extremity, which is usually bent or curled. Transverse sections (Pl. 18, fig. 12) show that the sacs arise ventrally close to the middle line; the connecting canal which unites the cavity of the sac with that of the œsophagus is extremely narrow within the œsophageal wall—only 2μ wide (in one instance I could not trace it at all), but still has a wall of its own constituted by epithelial cells.

Having become free of the wall of the œsophagus, the sacs are at first small, ventrally situated one on each side of the ventral vessel, which gives vessels to them and to the œsophagus; at first there are only one or two low ridges projecting into their interior (*gl. vii*). On passing forwards in the series of sections the sacs increase in size, attaining a diameter of 0.2 to 0.3 mm.—roughly half the diameter of the œsophagus (*gl. viii*); they become more dorsal,

and end, as already said, by tapering to a point. The number of ridges or lamellæ which project into the lumen increases with the diameter; the ridges run lengthways and are 10–12 or perhaps 14 in number in the main part of the sac, diminishing again to 5 or 6 in the narrow terminal portion. The ridges are unequal in height; the larger extend inwards almost to the central axis of the sac; they are quite simple in form, and, along with the whole of the sac-wall, are covered by a cubical epithelium (the œsophageal epithelium is columnar). Between the two epithelial layers of each lamella is a blood-space, continuous, it may be by a narrow neck, with the blood-sinus in the sac-wall. In transverse section the blood-spaces in the lamellæ are often irregular or moniliform (*gl. viii*); in the tapering terminal portion the lamellæ are almost devoid of blood.

The œsophagus in segments xiv and xv shows transverse vascular channels in its wall; it swells out suddenly and greatly in xvii to form the intestine. The first part of the intestine was filled in one specimen with a soft white mass, like a coagulum; microscopically the material was an amorphous granular substance without any structure. In a second specimen this part of the gut contained only a small quantity of a loose white matter, also structureless and granular under the microscope. The typhlosole in the anterior part of the intestine is a vertical lamella, slightly frilled—*i. e.*, its free border is somewhat longer than its attachment.

The last heart is in segment xiii (in three specimens dissected).

The nephridia are one pair per segment. There is no muscular sphincter (confirmed by transverse sections).

The testes (relatively large in the dissected specimens) and the funnels are free in segment xi; there are no testes or funnels in x. The seminal vesicles are a single pair, in xii or mostly in xii—the exact condition differed in the three specimens dissected. In the first they were small mulberry-like masses confined to xii, with crenated surface—the surface was cut up into a large number of small round lobules; in the second the lobulation was the same, but while the left vesicle was confined to xii, the right presented a narrow posterior prolongation which extended as far as segment xiv, with small bulgings in xiii and xiv; in the third the vesicles were confined to xii, were rather larger than in the other two (especially that on the right side), and the lobulation extended deeply, so that the vesicles might almost be described as racemose.

The vasa deferentia are visible on the body-wall as straight white cords running back a little external to the line of the ventral setæ, and ending on the anterior part of segment xviii in a small whitish area on each side; the white appearance is seen, on close examination, to be due to a number of small discrete structures lying on the body-wall. Microscopic sections show that these white dots are not, as I had supposed, groups of gland-cells discharging on the surface, but masses of fairly deeply staining cells with large nuclei, without any communication with the surface; these small cell aggregates lie deep to the muscular layer, and are covered over by or are sometimes continuous with the peritoneal layer; they appear to be of mesoblastic origin and not derived from the surface

epithelium. The sections show that the vas deferens remains small and inconspicuous to its end, and discharges into the crescentic groove on segment xviii, probably near the middle of the length of the groove, and in the anterior part of xviii, well in front of the level of the setæ. The proper glandular cells of the clitellum are absent on the ridges which bound the crescentic groove.

The ovaries and their funnels are in xiii; the oviduct leads to the neighbourhood of the ventral setæ of xiv, where it discharges on the surface.

I failed to find any trace of spermathecæ in the three specimens dissected.

The clitellar setæ (Pl. 18. fig. 13) are 0.22 mm. in length, with the usual sigmoid form, and possessing a nodule; they show an inconspicuous sculpturing, of a few scar-like markings, semicircular or horseshoe-shaped, the convexity of the curve facing proximally; the interior of the horseshoe appears to be slightly depressed. These markings are situated in the region of the distal curve of the shaft; about four are to be seen, some larger some smaller, on the side of the seta as it lies in the field of view.

Remarks.

The present species differs markedly from the two other members of the genus, *D. barbadensis* and *D. thomasi*. The calciferous glands, though not very large, are larger than in these species, where they are very small, or were at first actually overlooked. The last hearts are in xiii (not xi). The backward extension of the seminal vesicles is much less—I only found it, and then only to a slight degree and on one side, in one of the three dissected specimens, all of which had a perfectly well developed clitellum. Lastly, I found no spermatheca at all in any of the specimens—nothing was to be seen even within the transparent body-wall.

It is, of course, just possible that the comparatively small development of the seminal vesicles and the absence of spermathecæ are due to immaturity. Still, it seems that in view of the apparently complete development of the external sexual characters some trace of spermathecæ would have been present if the organs were going to develop at all.

The worms do not seem to feed on earth or mud, or even on vegetable debris; but what their normal pabulum may be I cannot say.

Finally, it may be noted that the present species occurs more than 2000 miles away from the other members of its genus, which are West Indian forms.

Subfamily MICROCHÆTINÆ.

Genus DRILOCRIS Mich.

DRILOCRIS sp.

159. Makthlawaiya, edge of swamp. 1. x. 26. Five specimens, none with external sexual marks.

160. Makthlawaiya. 1. x. 26. Several specimens, some fragmentary, none with external sexual marks.

895. Makthlawaiya, from mud at edge of swamp. xi. 26. Several specimens, one doubtfully showing the beginnings of sexual characters.

External Characters.

Length of well-grown specimens 78–108 mm. ; smaller specimens down to 35 mm. are also present. Average diameter of full-sized worms, 1.5 mm. at the middle of the body ; the largest specimen has a maximum diameter of 2.25 mm. in the anterior part of the body ; the posterior part of the body is tapering. Segments ca. 240, becoming very small and very short towards the hinder end. The anus is a longitudinal slit at the hinder end of the dorsal surface. The worms are unpigmented.

The prostomium is prolobous, short, broad at the base, rounded in front, but the groove which bounds it behind is very slight and is sometimes indistinguishable, so that the prostomium in these is zygotobous.

The body of the worms was apparently originally more or less four-sided, and square in transverse section behind the anterior segments, but the present specimens seem in many cases to have become flattened dorso-ventrally.

The setal couples, closely paired, are at the four corners of the body. Through the greater part of the body the four sides—dorsal, ventral, and lateral—are equal ($aa = bc = dd$). Towards the hinder end the dorsal surface becomes hollowed, and so forms a shallow groove ; the terminal region is curled dorsalwards, and the ventral side of the square transverse section becomes smaller than the dorsal, so that here aa is less than dd , and the sides of the body slope downwards and inwards.

In some specimens the dorsal groove at the hinder end of the body has its lips approximated, so that the groove is much narrowed and at the same time deepened. The ventral surface is not, in such a case, narrower than the dorsal.

No clitellum or sexual marks could be seen externally in any of the specimens, except in one where, very doubtfully, a clitellum seemed to extend from segment xvi to or nearly to the fiftieth segment. Sexual apertures were not distinguishable. There appeared to be slightly marked ventro-lateral ridges, just external to the lines of the ventral setæ, on segments xiv–xvi, which might possibly represent the beginnings of male copulatory organs, but I am doubtful about them, and think it quite likely that they are accidental.

The setæ are ornamented, showing a few fine points and transverse markings on the distal part of the shaft, in the region of the distal curve (Pl. 18. fig. 14).

Internal Anatomy.

No septa are markedly thick, but those in the anterior part of the body appear to be somewhat strengthened, perhaps as far back as xv.

There is no œsophageal gizzard, but the intestine is perhaps slightly strengthened at its commencement, in xv and xvi, or xiv–xvi, before it begins to be filled with earthy matter in xvii. There are no calciferous glands.

Hearts are present in segments vii–xi, large, tortuous, and moniliform.

Nephridia are not recognizable in front of segment xv.

Early stages of the genital organs were seen in dissections. The testes and male funnels were recognizable, free, in segments x and xi, and the ovaries and

female funnels in xiii. Moderate-sized seminal vesicles were present in xi and xii, only slightly cut up into lobes, and a pair of small empty sacs, perhaps supernumerary seminal vesicles, in xiii. There appeared to be a pair of ovisacs in xiv, and in one specimen a pair of smaller sacs in xv, and still smaller in xvi. In this specimen, therefore, there appears to be, perhaps as an individual abnormality, a continuous series of storage chambers for the sexual products in segments xi-xvi—an abnormality of the same kind as the numerous reported cases of supernumerary gonads, which may stretch in a continuous series for a number of segments backwards from segment x.

I could discover no spermathecæ, though I stripped up the longitudinal muscular coat of the body-wall throughout the genital region in an endeavour to recognize their beginnings.

Remarks.

Mr. Beadle notes on this worm "Groove at hinder end used for air breathing." The hollowing of the dorsal surface and formation of a longitudinal groove at the hinder end of the body, and the dorsal curling of the hinder end, are features of a number of Glossoscolecoid worms (*e. g.*, species of *Glyphidrilus* and *Criodrilus*); this worm was seen to carry down from the surface a bubble of air in the groove, which he thinks may thus have a special respiratory function.

Of the seven known species of the genus *Drilocrius* two have been found in Colombia, one in Ecuador, one in Costa Rica, and three in Brazil—one on the Amazon above Manaus and two in the State of São Paulo. The present species, to which I cannot give a name owing to the immaturity of the specimens and consequent imperfection of the description (especially as regards the male copulatory organs and spermathecæ, which furnish the most important diagnostic features), thus comes from a region from which the genus has not hitherto been recorded. It appears to differ from all previously described species in its dimensions; though presenting nothing peculiar in its length, it is remarkably slender, much slenderer, absolutely and relatively to its length, than any of the species hitherto known.

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Fig. 1

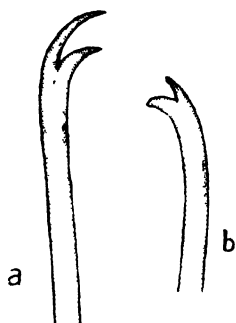


Fig. 2

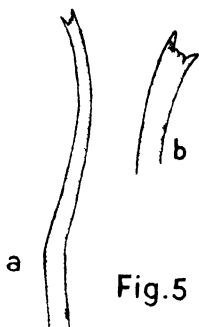


Fig. 5



Fig. 4

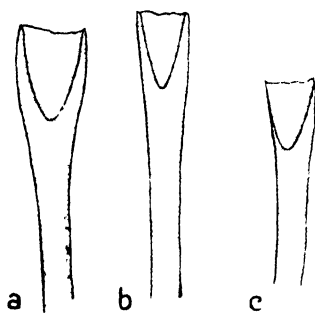


Fig. 3

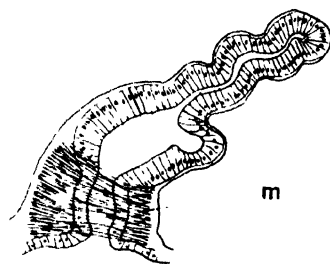


Fig. 7.

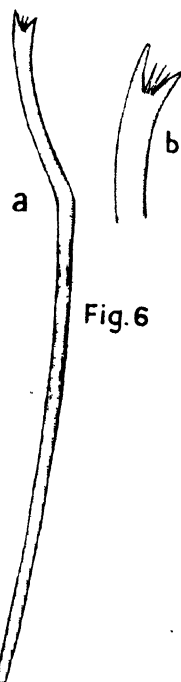


Fig. 6

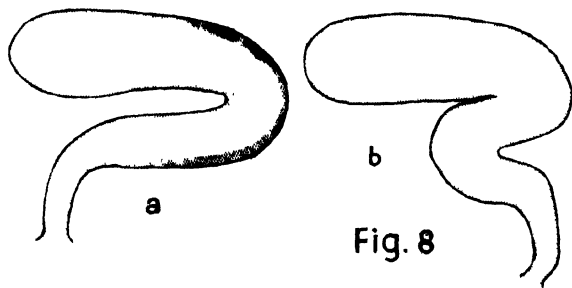


Fig. 8

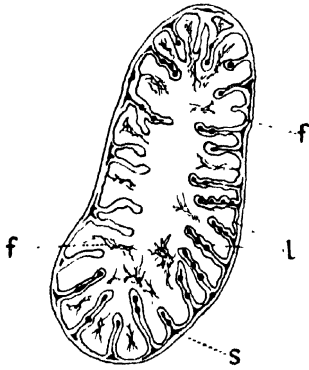


Fig. 9

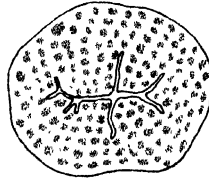


Fig 10 a



Fig. 13.

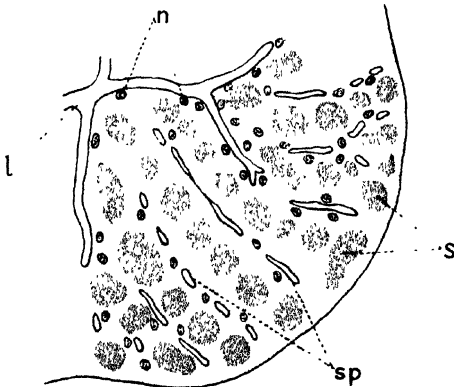


Fig. 10 b

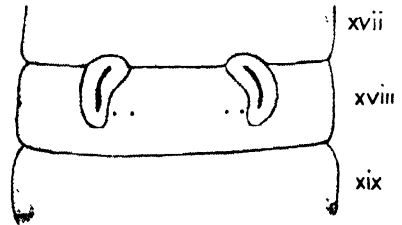


Fig. 11.

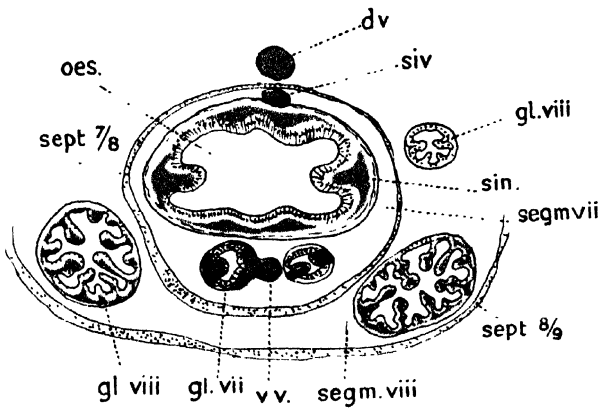


Fig. 12.

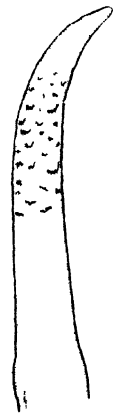


Fig. 14

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EXPLANATION OF THE PLATES.

PLATE 17.

- Fig. 1. *Nais pectinata*, dorsal needle-seta; \times ca. 2000.
2. *Aulophorus carteri*, ventral setæ: *a* of anterior segments (ii-v); *b*, of posterior segments; \times ca. 1250.
3. The same, dorsal needle-setæ; \times 1000.
4. *Aulophorus borellii*, dorsal needle; \times 700.
5. *Aulophorus beudlei*, dorsal needle-seta: *a*, \times ca. 1000. *b*, tip more highly magnified ca. 2250.

- Fig. 6. *Aulophorus pectinatus*, dorsal needle-seta; *a*, $\times 880$; *b*, tip more highly magnified. ca. 1750.
7. *Kerria limosa*, spermatheca, in longitudinal section (reconstructed from several sections); *m.*, the very strong layer of circular muscular fibres round the duct.
8. The same, spermatheca, showing two forms.

PLATE 18.

- Fig. 9. *Kerria limosa*, calciferous gland in transverse section: *f*, floccular or fibrillar matter in cavity; *l*, lamella containing moniliform (in section) blood-space; *s*, peripheral blood-sinus.
10. *Kerria pascuorum*, calciferous glands.
- 10*a*. Transverse section under low power ($\times 150$), diagrammatic.
- 10*b*. A portion of the same more highly magnified ($\times 450$), semidiagrammatic. *L*, star-shaped lumen; *n*, nuclei; *s*, blood-sinuses; *sp*, spaces in substance of gland, probably indicating planes of separation between fused lamellæ.
11. *Diucheta ead.*, male field, ventral setæ of segment xviii indicated.
12. The same, part of a transverse section through the region of the calciferous glands. The septa are here cone-shaped, the glands of segment vii are cut close to their origin from the œsophagus, those of viii are cut through their middle, with, in addition, the recurved end of one shown on the right side of the figure. *D.v.*, dorsal vessel; *gl. vii*, the calciferous gland of the left side of segment vii, at its hinder end close to its origin; *gl. viii*, the gland of the left side of segment viii, cut through its middle, and the gland of the right side cut through near its (reflexed) termination; *œs.*, the œsophageal lumen; *segm. vii*, the cavity of segment vii; *segm. viii*, the cavity of segment viii; *sept. 7/8*, the septum separating segments vii and viii; *sept. 8/9*, that between segments viii and ix; *sin.*, alimentary blood-sinus in œsophageal wall; *sv.*, supra-intestinal blood-vessel; *v.v.*, ventral vessel, connected with the glands of segment vii near their origin.
13. The same, genital seta, distal half.
14. *Drilocrius* sp., a seta, distal portion.

Reports of an Expedition to Brazil and Paraguay in 1926-7, supported by the Trustees of the Percy Sladen Memorial Fund and by the Executive Committee of the Carnegie Trust for the Universities of Scotland.

The Fauna of the Swamps of the Paraguayan Chaco in relation to its Environment.—II. Respiratory Adaptations in the Fishes. By G. S. CARTER, Ph.D., F.L.S., Lecturer in Zoology in the University of Glasgow, and L. C. BEADLE, B.A., Pembroke College, Cambridge. (Communicated by Dr. G. P. BIDDER.)

(PLATES 19-23, and 5 Text-figures.)

[Read 18th April, 1929.]

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INTRODUCTION.

The subject of aerial respiration in the fishes, with which this paper deals, is of interest to the biologist from many points of view. It provides an example of a fundamental change in the functioning of one of the main physiological systems of the body, and it is therefore of interest in the study of the physiology of fishes in general. It is of especial interest from this point of view, because it is a change which has occurred very frequently and in many different ways. It is also a change which must have occurred in the sequence of adaptations which made possible the migration of the fishes from the water to the land. It

is therefore of interest in the study of the evolution of the vertebrates at this point. The facts recorded in this paper and in the preceding one (1930 *b*) will be found to indicate that this adaptation was probably the starting-point of the whole sequence of changes which resulted in the migration ; that it occurred while the fish was still purely aquatic, in response to the conditions of the aquatic environment ; that it was not primarily an adaptation for the purpose of leaving this environment, but that it favoured the migration by putting the fish in a favourable position for the later changes which were definitely associated with the migration.

The interest of this subject from the point of view of the series of papers of which this is one, is again different. These papers are intended to give an account of the bionomics of one type of freshwater environment. The occurrence of an adaptation such as that of aerial respiration in the fauna of this environment may be expected to throw some light upon the conditions to which the fauna is exposed, and to confirm or refute the conclusions derived from direct observation of these conditions. Any type of peculiar adaptation must always be of interest in bionomic investigations.

The fresh waters discussed in these papers are certain swamps in the Paraguayan Chaco. In the previous paper the results of a series of observations upon certain of the physical and chemical conditions to which the fauna is exposed in these swamps were given. The swamps are typical examples of a shallow and stagnant freshwater exposed to a tropical climate, and it was the conditions of life in this environment that it was hoped by means of the investigation to define. The most general conclusion of these observations was that the low concentration of dissolved oxygen is the condition of greatest bionomic importance in these waters. It was found that the lower layers of the water are often without any measurable quantity of oxygen, and even that within half an inch of the surface often contained less than 0.1 c.c. per litre (2 per cent. of the saturation value). Conditions of this type occurred during the hot weather and often lasted for many days.

The fauna of the swamps is considerable and varied, but is never rich. When the nature of the conditions of the environment had been determined, the manner in which the fauna is able to live under these conditions became a subject for investigation. Investigation showed that most of the fauna is peculiarly adapted in one way or another to life in a medium poor in oxygen. It is intended to discuss these adaptations in the succeeding papers of the series.

The fauna includes representatives of almost all the groups of freshwater animals, but not all of these are of interest in this discussion. All fresh waters contain many animals whose respiration is aerial and not aquatic. Such animals can only live in an aquatic medium by carrying with them a supply of oxygen obtained from the air above the water. To them the amount of oxygen in the water itself is unimportant. For this reason, all the higher vertebrates, and, with few exceptions, the insects and their larvæ, very numerous in these

swamps as in most other fresh waters, need not concern us. Of the remaining groups, the smaller Crustacea (Cladocera, Ostracoda, Copepoda, and Amphipoda) and the Rotifers were sometimes present in considerable numbers, and a few Oligochaetes were to be found. The most strikingly abundant animals were the fishes. Their respiratory adaptations are the subject of this paper.

The following twenty species of fish were collected in these swamps* :—

<i>Hoplias malabaricus</i> Bloch	Common.
<i>Erythrinus unitaeniatus</i> Spix	"
<i>Tetragonopterus nigripinnis</i> Perugia	"
" <i>agassizii</i> Boulenger	"
<i>Serrasalmo spilopleura</i> Kner	Occasional.
<i>Pyrrhulina australis</i> Eigenmann & Kennedy	Common.
<i>Characidium fasciatum</i> Reinhardt	"
<i>Hypopomus brevirostris</i> Steindachner	"
<i>Rhamdia quelen</i> Quoy & Gaimard	Frequent.
<i>Trachycoristes striatulus</i> Steindachner	"
<i>Callichthys callichthys</i> Linn.	"
<i>Hoplosternum litorale</i> Hancock	Common.
" <i>pectorale</i> Boulenger	"
<i>Ancistrus anisitsi</i> Eigenmann & Kennedy	Occasional.
<i>Loricaria typus</i> Bleeker	Frequent.
<i>Rivulichthys rondoni</i> Ribeiro	Common.
<i>Crenicichla lepidota</i> Heckel	Rare.
<i>Acara portalegrensis</i> Hensel	Common.
<i>Symbranchus marmoratus</i> Bloch	"
<i>Lepidosiren paradoxa</i> Fitz.	"

With the exceptions of *Serrasalmo spilopleura*, the piranha of the Brazilians and the palometa of the Argentines, and of *Crenicichla lepidota*, these fish live in the swamps at all times of the year, and are therefore true members of the swamp-fauna. The piranha is typically a fish of the larger rivers and lagoons, and only invades the swamps after heavy rain, when they are flooded and their water contains much more oxygen than at other times. *Crenicichla lepidota* is also only an occasional visitor to the swamps. It is rare, and we were not able to study its habits. These two species will not be further considered in this paper.

There are two sources from which animals living in poorly oxygenated water may obtain oxygen. In the first place and most obviously, there is the rich supply in the air above the water. In order that a fish may make use of this supply, some adaptation to aerial respiration is necessary, and the most striking characteristic of the fishes of these swamps is the large proportion of them which are so adapted. Of the twenty species in the list given above, eight belonging to seven genera are able to breathe air. These are the representatives of the genera *Erythrinus*, *Hypopomus*, *Callichthys*, *Hoplosternum*, *Ancistrus*, *Symbranchus*, and *Lepidosiren*. Further, the adaptations in most of these genera

* We are indebted to Mr. J. R. Norman, B.Sc., for the identification of these fish, and for much help in the course of the investigation.

are independent in type and origin. Only *Hoplosternum* and *Callichthys* are closely related forms. They are also very similarly adapted. There can therefore be no doubt that their adaptations represent a single phylogenetic type. All the other genera are distantly related, both to each other and to these two. Their adaptations are also distinct. We have therefore six independent forms of air breathing among these fishes.

The other available source of oxygen lies in the very shallow surface layer of the water. It has been stated that all layers of the water to within half an inch of the surface are often almost completely without oxygen. It is not possible to determine the conditions in the surface layer itself owing to its thinness, which prevents the collection of water from it for analysis; but it is in close contact with the air, and is probably well oxygenated. That it contains more oxygen than the lower layers of the water is made evident by the behaviour of the fish. All the species which have not the habit of breathing air use this layer as a source of oxygen. They can be seen lying below the surface and drawing the water from the surface over their gills. Some (*Tetragonopterus* spp., *Pyrhulina australis*, *Acara portalegrensis*, etc.) remain in this position for many minutes together, and others (*Rivulichthys rondoni* etc.) pay frequent short visits to the surface.

By this means some species are able to survive under any conditions, provided that the swamp or pool in which they are living does not dry completely. Many (e.g., *Rivulichthys rondoni*, *Characidium fasciatum*) may be found in pools and holes in which the water is rapidly evaporating and very foul. Often none of the water of a pool containing many fish, except presumably the surface layer, contained oxygen in sufficient quantity for measurement. But this habit gives no protection against the frequent periods of drought in which the swamps and pools dry up over large areas of the country and no standing water is left. It is therefore a less complete adaptation to the conditions of the environment than the aerial respiration, which, in *Lepidosiren* and *Symbranchus*, makes it possible for the fish to live through these periods in burrows, and, in *Callichthys*, to migrate over the grassland in search of a new pool.

It would seem that this method of respiration should be more readily available for a small fish than for a large one, and most of the fishes which were observed to make use of it were small. But some large fish also have this habit. *Hoplias malabaricus* reaches a length of 12 inches and is among the largest fishes to be found in these swamps. It often comes to the surface and lies there for some seconds, drawing a current of water from the surface layer over its gills. It never swallows air. It can be drowned if it is prevented from reaching the surface in poorly oxygenated water, but it lives well under the same conditions if the water is well oxygenated. It is common in the swamps at all times, and its survival is undoubtedly due to its habit of using the surface layer as a source of oxygen.

Other fishes of these swamps which reach a large size but do not breathe air are *Trachycoristes striatulus*, *Rhamdia quelen*, and *Loricaria typus*. We were

not able to observe the habits of these fish. It is possible that more complete observations than we were able to make would add the last of these to the list of air-breathing fishes.

The habits of *Lepidosiren* and the structure of its lungs have been described by previous authors (Graham Kerr, 1900, etc.; Hunt, 1898). Some new observations upon its habits have been recorded in another paper (Carter & Beadle, 1930 a). Its adaptations will not be further discussed here. The occurrence of air-breathing in *Symbranchus* and its adaptations to aerial respiration are also well known (Taylor, 1913), and need no further description. There remain four types of aerial respiration among these fishes—those of *Erythrinus*, *Hypopomus*, *Callichthys* and *Hoplosternum*, and *Ancistrus*. Many years ago Jobert (1877, 1878) described aerial respiration in species of *Erythrinus* and *Callichthys* among other Brazilian fishes, but his observations have not been always accepted, and no accurate description was given of the accessory respiratory organs in these genera; they will therefore be described in this paper and some new observations on the physiology of these fishes will be given. No previous account of aerial respiration in *Hypopomus* and *Ancistrus* is known to the authors; the adaptations of these genera will be described.

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CHARACINIDÆ.

ERYTHRINUS UNITÆNIATUS Spix. (Pl. 19.)

The lung-like structure of the air-bladder in this fish was first noted by Cuvier and Valenciennes (1837) almost a century ago. The suggestion that it serves as a respiratory organ was made almost as soon as its structure had been described. Thus Joh. Müller in 1841 refers to the suggestion, and dismisses it on the ground that the blood reaches this organ by an artery, whereas, in his opinion, the supply of a respiratory organ must always be by a vein. This opinion has not been borne out by later work on the accessory respiratory organs of fishes (see pp. 354-355). It does not allow for the possibility that arteries may sometimes contain venous blood.

Cuvier and Valenciennes gave figures of the inner and outer aspects of the wall of the bladder, and several authors have followed them in description and discussion of its external features. Its internal structure has been much less completely described: de Beaufort (1909) mentions the presence of thin-walled cavities or cells in the thickness of the wall, but he does not describe them in detail and we have been able to find no other account. The only work upon the physiology of the bladder is due to Jobert (1878). This author investigated three species of the genus as it was constituted according to his authorities,

namely, *E. taeniatus* Spix, *E. braziliensis* Spix, and *E. trahira* Spix. He states that in the first two of these the bladder is cellular and serves as a respiratory organ, but that in the third the cellular structure is absent and the respiration is carried on in other ways *. He observed that the two species in which the bladder is cellular had the habit of coming to the surface and taking mouthfuls of air. He found that they died in a short time when they were prevented from reaching the surface, presumably in poorly oxygenated water (see p. 334). He opened the body-cavity and ligatured the pneumatic duct. Again, death quickly followed. These last experiments have been criticised by Sørensen (1884) and Bridge and Haddon (1894) on the ground that the ligature may also have bound branches of the vagus nerve and that death may have been due to this cause. His other experiments gave no proof that the air taken in at the mouth reached the bladder. His conclusion that the bladder is respiratory has not been generally accepted.

We were unable to collect embryological material of this fish, and its breeding habits are unknown to us. It is common in these swamps at all times of the year.

Adult Structure.

When the body-cavity is opened, the air-bladder is seen to extend throughout the whole length of the cavity and to occupy more than one-half of its space (Pl. 19. fig. 1 *a; b*). It is clearly divided into three parts. The outside of the wall of the anterior and posterior of these is smooth and has a white sheen. That of the central part is highly vascular and has very much the appearance of a lung. This is due in part to the red colour given to it by its rich blood supply, and in part to the outlines of the cavities, immediately to be described, which lie in the thickness of the wall. Seen through the thin outer sheath, they greatly resemble a similar view of the alveoli of a lung.

The central part of the bladder is separated from the anterior by a deep circular groove, which surrounds a comparatively narrow opening. It passes into the posterior part without any alteration of diameter. A wide pneumatic duct (Pl. 19. fig. 2, *pn.d.*) opens into the bladder in the ventral line at the front end of its central part, and into the alimentary canal slightly further forward. The opening of this duct into the alimentary canal on the left side of the median plane has been much discussed.

The inner surface of the wall of the anterior and posterior parts of the bladder is smooth, and the wall itself thin. The wall of the central part is very different. A shallow ridge (*d.r.*) runs along the inner surface in the dorsal line, and another,

* There appears to be confusion in the identification of these species. *E. braziliensis* Spix and *E. trahira* Spix are both given by Eigenmann (1910) as synonyms of *Hoplias malabaricus* Bloch, in which genus the bladder is not cellular. *E. taeniatus* Spix should presumably read *E. untaeniatus* Spix, the species described in this paper. It would seem that *E. braziliensis* should be grouped with *E. trahira* and not with *E. taeniatus* or *untaeniatus*.

less well defined, in the ventral line. These are joined by a series of transverse ridges (*i.r.*) around the inside of the wall. These transverse ridges are not entirely regular; some pass only a part of the way round the wall and join those in front or behind them. Lower and thinner cross-ridges are present everywhere between the transverse ridges. The surface is thus divided into numerous, generally square, cells.

In a view of its inner surface the thickness of the wall cannot be appreciated. The complete structure is better seen in a transverse section of the bladder (Pl. 19, fig. 3). This section shows that the shallow cells between the internal ridges (*i.r.*) are only the outer layer of a thick mass of similar cells, which occupies the greater part of the thickness of the wall. The septa between these cells are very thin and the whole mass has the appearance of a foam. The space occupied by them is greatest in the lateral line of the bladder. Near the dorsal and ventral lines it becomes much reduced and only one layer of the cells is present.

The cellular internal structure of the wall is found over the whole length of the central part of the bladder. The cells open into each other by wide openings (*o.*, 0.1–0.4 mm. in diameter), and on the inner side into the spaces between the internal ridges. The outer covering of the bladder is a thin and fibrous sheath.

The arrangement of the blood-vessels supplying the central part of the bladder is shown in figs. 1 and 3 (Pl. 19). Jobert (1878) stated that this part of the bladder is supplied by the coeliac artery and the interrenal vein. It will be seen that our dissections confirm this. A large branch of the coeliac artery (Pl. 19, fig. 1, *c.a.*) passes along the right ventral side of the anterior part of the bladder and reaches the groove behind it in the ventral line. From this point two branches pass up the front wall of the central division to the lateral line. There they turn backwards and run along the lateral line of the bladder to its posterior end (*r.a.*).

The blood from this part of the bladder is collected by veins in the lateral line on each side (*r.v.*). These veins lie alongside the arteries, and are sometimes ventral and sometimes dorsal to them. At the front end of the central division of the bladder they pass up the wall to the dorsal side and there join. With veins from the hinder part of the body they form the large interrenal vein (*ir.v.*) which passes along the roof of the body cavity, dorsal to the anterior division of the bladder, and then ventralwards down the anterior wall of the cavity to join the right ductus Cuvieri.

In the wall of the central part of the bladder these veins and arteries lie just below the surface of the outer sheath (Pl. 19, fig. 3, *r.a.*, *r.v.*). From both, dorsal and ventral transverse vessels (*t.v.*) arise in the wall of the bladder. These are far more numerous where the wall is cellular, but they are also present in the hinder part of the bladder. Smaller arteries and veins pass from the transverse vessels into the septa between the cells. The distribution of the veins (*s.v.*) in a segment of the wall of the bladder is shown in fig. 3 (Pl. 19). Their

thickness is exaggerated in this figure in order to make their distribution clear. It will be seen that they pass through the whole thickness of the cellular layer, and reach the cells immediately adjacent to the internal ridges. The distribution of the arteries is similar to that of the veins.

Histology.

The thinness of the transparent septa between the cells in the wall of the central part of the bladder is remarkable. Sections through small pieces of these septa are shown in fig. 4, *b* and *c* (Pl. 19), and it will be seen that their thickness never exceeds 10μ and is often considerably less. Almost everywhere the septum is formed by a single layer of pavement epithelium (*p.ep.*). Many of the cells of this epithelium are Y-shaped in section and enclose capillaries between them. Occasionally places can be found where two epithelial cells lie over each other (Pl. 19. fig. 4, *c*, *ep.*'). These are along the edges of capillaries, which, in section, are therefore bounded by three cells. These places are comparatively rare. It is clear that the septum must have been evolved from a wall at least two cells thick, and it is possible that in these places we have the last trace of the second layer of epithelium.

The presence of capillaries in these septa is shown in the sections just described. A surface view of the septum (Pl. 19. fig. 4, *a*) shows that the capillary network is dense. The structure of the septum is the same throughout the central part of the bladder, and the capillary network is present everywhere.

Thus the structure of these septa is very simple. It probably provides great respiratory efficiency. Although the capillaries are generally closer to one side of the septum, its thinness must allow respiration to go on through both sides of the capillary. In this feature it is nearer to the gills of the fishes than to the lung of a terrestrial mammal, in which only one side of the capillary is brought close to the air of the alveolus. The wide openings of the cells into each other and into the central lumen of the bladder must allow rapid diffusion of the gases contained in them.

Behaviour and Physiology.

Erythrinus unitaeniatus dies within 2-3 hours if it is placed in water containing little oxygen and prevented from reaching the surface. If it is not prevented from doing so, it will live indefinitely in water almost completely without oxygen. Whatever the nature of the water in which it is, it frequently comes to the surface and takes in air at the mouth, if it is allowed to do so. Much of this air escapes immediately at the gill opening. Bubbles are also given out either at the mouth or at the gill opening in the interval between one visit to the surface and the next. These bubbles clearly consist of air exhaled from the respiratory organ.

We were able to show that that part of the air which is swallowed and does not immediately escape is passed to the air bladder, and is not retained in the mouth or the gill chamber. That this should be so, it is necessary that the

pneumatic duct should be open. In *Erythrinus* the duct is very wide, and it is easy to force air down it into the alimentary canal by pressure on the wall of the bladder. It is therefore a possible passage for air into the bladder. To show that air is normally passed along it, the side of the body of a living fish was opened and the wound held open by a prop. The central part of the bladder was then pierced, and the fish was returned to the water in which it had been living. It was apparently little disturbed by the operation and lived for many hours. At first its behaviour was normal. It took in air at the mouth in the usual way, but, whenever it did so, bubbles were seen to escape at the puncture in the wall of the bladder. The bladder was full of air throughout the experiment, but bubbles did not come out of it at other times owing to the smallness of the puncture. This result seems to prove that the amount of gas in the bladder is increased whenever air is swallowed, and therefore that air is passed into the bladder along the pneumatic duct.

For a time the behaviour of the fish remained normal, but later (about 30 minutes after the operation) it was observed that it began to come to the surface more frequently. After two hours it was doing so every 10 seconds, the normal interval being about 10 minutes. It lived for many hours after this and was apparently healthy. The more frequent visits to the surface may have been due to its inability to keep the pressure in the bladder above that of the atmosphere. In the normal fish a slightly higher pressure is maintained.

It remains to show that respiration takes place in the bladder. To do this we analysed samples of gas taken from the bladder. The following method of analysis was used.

A fish was taken from the tank in which it had been living and killed suddenly by a blow upon the head. The side of the body was then opened under water as quickly as possible and a bubble of gas from the bladder brought into a narrow glass tube, closed at one end, by means of a small funnel. The length of the bubble was measured. Caustic potash was then added to the water in the tube, and it was shaken by moving the bubble up and down it several times. It was found that any carbon dioxide in the gas was quickly absorbed. The bubble was again measured. Then crystals of pyrogallie acid were added to the water in the tube, which was already alkaline owing to the addition of caustic potash. It was found that all the oxygen was absorbed, when the tube was again shaken. A final measurement gave the data for the calculation of the constitution of the mixture.

Using a long bubble to minimise the error due to its hemispherical ends, and correcting for this error as accurately as possible, we found that it was possible to estimate the constitution of the mixture by this method to within 1 per cent. with regard to either of the two gases. It had several advantages. As only a small quantity of the gas was required for the estimation, it was possible to apply the method to small fishes. Further, the analysis could be made rapidly. In most of the older methods of analysis the mixture was allowed to remain in contact with water for a long time before the proportions

of the two gases were estimated. If this is done, the proportions may be greatly altered by solution in the water, the solubilities of the gases being very different. We were able to estimate the composition within a few minutes of the time that the gas was taken from the bladder. It is possible that some carbon dioxide may have been dissolved during the analysis, and that the values of the carbon dioxide content are therefore too small. Oxygen is much less soluble in water, and it is unlikely that the proportion of it was appreciably altered. In the absence of apparatus for accurate gas analysis, the method seemed to give the most reliable results attainable. It was tested in various ways—*e.g.*, by the analysis of atmospheric air.

Five analyses of gas taken from fish which had been in a tank of water for some hours in a healthy and normal condition, and had been continually taking air at the surface, gave proportions of oxygen varying from 5.8 to 8.5 per cent. and of carbon dioxide from 0 to 2.8 per cent., the average being 7 per cent. of oxygen and 0.7 per cent. of carbon dioxide. Thus the composition of the gas in the bladder is very different from that of air (21 per cent. of oxygen and 0.3 per cent. of carbon dioxide). The gas is continually renewed from the air, and this difference must result from the activities of the tissues of the fish. It indicates a very considerable absorption of oxygen and some excretion of carbon dioxide.

It has been stated that the fish dies if it is prevented from reaching the surface in *poorly oxygenated water*. Under these circumstances gas will be enclosed in the air bladder and the fish will have no opportunity of renewing it. It is therefore to be expected that exchange would go on continuously between this gas and the blood, and that after some time its composition would show a greater difference from that of air than is shown by the gas in the bladder of a normal fish. Three analyses of gas taken from fish, which had been kept from the surface for 2–3 hours, and were on the point of death, gave results varying from 4.5 to 0 per cent. of oxygen and 2.0 to 0.9 per cent. of carbon dioxide (averages 1.8 per cent. of oxygen and 1.5 per cent. of carbon dioxide). These results confirm those of the experiments on normal fish.

Thus it is clear that the air bladder is an accessory respiratory organ. It is easy to show that all the respiration of the fish is not carried out in this organ. This is indicated by the disproportion shown by these experiments in the amounts of the respiratory exchange of oxygen and carbon dioxide. The total respiration of these fish will be further discussed below (p. 358). We have some experiments to record which show that the other respiratory organs, presumably mainly the gills, but also the skin, if this is effective, are sufficient to maintain life when the fish is prevented from using its air bladder, provided that the water in which the fish is living is *well oxygenated*.

A fish was placed in a tank in which the water was kept well oxygenated throughout the experiment. This was done by arranging a spray of fresh water on the surface of the water in the tank. To ensure that the water was renewed in all parts of the tank, the level was maintained by a siphon which reached

to the bottom of the tank. The fish was prevented from reaching the surface by wire-netting, and care was taken that no bubbles from the spray reached the level of the netting. With this arrangement, the water in the tank never contained less than 4 c.c. per litre of oxygen. At the time, the temperature of the air was 30–35° C., a not unusual temperature for the waters in which the fish habitually live. At this temperature, water is saturated with 5.55 c.c. per litre of oxygen. The oxygen content of the water in the tank was therefore not far from saturation.

After it had been twelve hours in this tank the fish was healthy and showed no signs of discomfort.

At the end of two experiments of this type the fish was killed and the gas of the bladder analysed. In both cases it was found to contain no measurable quantity of oxygen. Almost all the oxygen present in the bladder at the beginning of the experiment must therefore have been absorbed, and the respiration carried on by the other respiratory organs of the body. This result makes it clear that these organs are able to carry out sufficient respiration for healthy life in this species, provided that the water is rich in oxygen.

The very small amount of oxygen in the gas at the end of these experiments is extraordinary and contrasts with the presence of a small but measurable amount in the bladders of fish which were dying from suffocation in poorly oxygenated water. It may be suggested that the long period of the experiment (12 hrs.) gave time for the absorption of the last traces of oxygen from the gas, and that the more rapid death of the fish in the poorly oxygenated water (after 2–3 hrs.) occurred before absorption was complete: but the periods are long in both types of experiment and it seems unlikely that this is the complete explanation. However this may be, the absence of any oxygen in the bladder of fish, living healthily and without discomfort, is not easy to explain, if the gas is simply in equilibrium with the blood. It must be noted that this result is based on only two analyses and that more experiments might show the presence of some oxygen. We have no data on the minimum concentration of oxygen in the medium which will maintain life in this fish.

STERNARCHIDÆ.

HYPOPOMUS BREVIROSTRIS Steindachner. (Pl. 21.)

This fish is common in the swamps of the Chaco at all times of the year. It is the only one of the four described in this paper, which, at first sight, shows no marked structural adaptations to the habit of breathing air. There can be no doubt that it has this habit and that it makes use of it in its life in the natural environment. We kept two examples (about 4 inches long) in a glass tube 1½ inches in diameter and containing about 100 c.c. of water. They lived for a week in a healthy condition in the tube, visiting the surface at intervals of 2–4 minutes to take mouthfuls of air. They were then prevented from reaching the surface by a wad of cotton-wool, which was placed in the tube below the surface of the

water. They showed distress within a quarter of an hour and died in 4 hours. Others were treated in the same way, but were allowed to come to the surface, when they were on the point of death, by removal of the cotton-wool. They recovered quickly.

In well oxygenated water the fish can live by aquatic respiration, but it always comes to the surface and swallows air when it is allowed to do so, whatever the nature of the water in which it is living.

The air bladder has a narrow duct, down which air could not be forced by pressure on the bladder. Analysis of gas taken from the bladder showed 2.7 per cent. of oxygen and 2.7 per cent. of carbon dioxide. This small proportion of oxygen in the bladder of a fish, which had not been subjected to any abnormal conditions, makes it unlikely that the air in the bladder is renewed by interchange with that taken in at the mouth. The bladder shows no peculiar structural modification. For these reasons it is improbable that it is used as an accessory respiratory organ.

It is easy to show that at least the greater part of the air is passed to the gill chamber. In a living fish the opercular region can be seen to be swollen after air has been taken, and to collapse when it is given out, which is always by the gill opening. If the operculum is pierced, bubbles of air escape at the puncture.

It must be concluded that the accessory respiratory organ lies in the gill chamber or is in communication with it. Dissection showed no peculiar organs opening out of the gill chamber or the neighbouring parts of the pharynx, such as occur in many air breathing fishes (*Anabas*, *Clarias*, *Periophthalmus*, etc.). The wall of the gill-chamber or the gills themselves are therefore the only organs which can serve the function of aerial respiration.

An examination of the gill chamber shows that it is particularly large in this fish, and extends so far ventrally towards the middle line that the space between the two chambers is reduced almost to the dimensions of a septum (Pl. 21. fig. 7). Except on the gills, the epithelium of the wall of the chamber is not abnormally vascular and does not appear to be respiratory. Only the gills remain as a possible seat of the respiratory function.

The lamellæ are long and spread through most of the chamber, but they are otherwise normal in structure. Their most obvious feature is the great development of the secondary folds, with which the respiratory lamellæ of the gills of fishes are provided. These are of the usual plate-like form extending across the breadth of the lamella. They are thin (10 μ in thickness) (Pl. 21. fig. 8), and have the typical structure of these folds, the blood circulating in lacunar spaces between pillar cells, which support the epithelium of the sides of the folds, rather than in true capillaries (Faussek, 1902, and Pl. 21. fig. 8, *b*). It is in the distance that the plate projects from the lamella that these folds differ from those of most fishes. In *H. brevirostris* the thickness of the fold, when it is seen in a longitudinal section through its broadest part (Pl. 21. fig. 8, *a*), is about 1/25th of its breadth from its attachment to the lamella to its

outer edge. It is not easy to compare this ratio with the same ratio in other fish on the basis of the figures of sections of the folds which have been given by previous authors. Usually in the sections figured the epithelium on the two sides of the fold has separated from the pillar cells, presumably owing to bad fixation due to the early date of the investigations (Riess, 1881; Droscher, 1882; Faussek, 1902). It appears that in most of the fishes which have been examined (and they are few) the breadth of the fold is about 7-8 times its thickness (pike, perch, roach, etc.). In *Hippocampus* (Riess, 1881), where the structure of the gills is peculiar and the folds are described as being broader than in other fish, the breadth is about 15 times the thickness. Only in the pseudobranch of the perch (Riess, 1881) have broader folds than those of the gills of *Hypopomus brevirostris* been found. In them the breadth is 30-35 times the thickness*.

In order to compare these folds more thoroughly with those of other fish, sections of the gill-lamellæ of a series of fishes from the Paraguayan Chaco were cut. In the fishes which do not breathe air the breadth of the fold was found to vary from 10 to 18 times its thickness. The average value of the ratio was 13.5. The ratios for the different fish are given in the following table:—

	Ratio.		Ratio.
<i>Hoplias malabaricus</i>	18	<i>Trachycoristes striatulus</i>	16
<i>Tetragonopterus</i> sp.	16	<i>Loricaria typus</i>	10.5
<i>Pyrhulhua australis</i>	10	<i>Rivulichthys rondoni</i>	11.6
<i>Characidium fasciatum</i>	14.5	<i>Acara portalegrensis</i>	11.6

In each fish, measurements were made of sections through the middle of the fold and through the broadest folds which could be found.

All the fishes (except *Erythrinus unitaeniatus*) which possess accessory respiratory organs in other parts of the body have distinctly narrower folds than the fish which do not breathe air. The ratios for these fish are as follows:—

	Ratio.		Ratio.
<i>Erythrinus unitaeniatus</i>	14	<i>Callichthys callichthys</i>	5
<i>Hoplosternum littorale</i>	1.1	<i>Ancistrus anisitsi</i>	6
.. <i>pectoralis</i>	6		

The gill-lamellæ of *Lepidosiren paradoxa* are very abnormal. It is not possible to compare folds upon them with those of other fish.

* It is clear that this ratio does not give a direct comparison of the area of the respiratory epithelium in the different fishes, but it seemed that in this way the respiratory efficiency of the epithelium in the different fishes could be best compared. The efficiency will be increased both by decrease in the thickness of the fold and by increase in its breadth. Therefore any increase in the ratio must be accompanied by increase in the efficiency of the epithelium.

It is noticeable that the folds are narrowest in *Hoplosternum litorale*, in which the respiration of the gills is least efficient and insufficient to maintain life under any conditions (see below, p. 346).

Further, five fish belonging to the Sternarchidæ and neighbouring families were examined*. In them the values of the ratio were found to be as follows :—

	Ratio.
<i>Rhamphichthys rostratus</i> (Linn.)	9
<i>Hypopomus occidentalis</i> (Regan)	8
<i>Eigenmannia virescens</i> (Valenciennes)	20 (P)†
<i>Gymnotus carapo</i> Linn.	20 (P)†
<i>Sternogypus macrurus</i> Bloch & Schneider	9

Thus in none of all these fishes are the folds as broad as in *H. brevirostris*. The use of the gills as organs of aerial respiration is not known to occur elsewhere among fishes, except possibly in *Symbranchus marmoratus*‡. The folds on the lamellæ of *Symbranchus* were examined and were found to be even broader than those of *Hypopomus brevirostris*. The breadth in this case was found to be 30–35 times the thickness.

It therefore seems that the development of aerial respiration in the gill-lamellæ is associated with an increase in the ratio of the breadth of the fold to its thickness. This must result in an increase in the efficiency of the respiratory epithelium.

It will be observed that the average breadth of these folds is greater in the fishes from the swamps of the Chaco, which do not breathe air, than has been found by previous authors to be normal in fishes. This fact suggests that the broadening of the folds is a development which occurs frequently in the fishes of shallow tropical waters in response to the lack of oxygen in the medium, and that it is not primarily associated with the breathing of air. This is very probably so, but, from the condition of these folds in *Hypopomus brevirostris* and *Symbranchus marmoratus*, it appears that a greater broadening of the folds than is usual is necessary, if the gills are to be used as organs of aerial respiration. It is possible that this type of aerial respiration will be found to be commoner in the fishes of tropical waters than the data at present available indicate. Owing to the absence of any other structural adaptation in such fish, examination of preserved material would not suggest the occurrence of aerial respiration. Observations on the living fish would be necessary, and have so far been rare.

* We are indebted to Mr. J. R. Norman for material of these fish.

† The length of the folds in these fish could not be accurately determined.

‡ *Symbranchus marmoratus* possesses no well developed accessory organ of aerial respiration. Yet it undoubtedly breathes air. The epithelium of the gill-chamber and the neighbouring parts of the pharynx is respiratory, and there is a small vascular pit in the pharyngeal wall above the openings of the gill-chamber. Probably aerial respiration is carried on by all these epithelia and by that of the gill-lamellæ. (See Taylor, 1918.)

CALLICHTHYIDÆ.

HOPLOSTERNUM LITORALE Hancock. (Pls. 21 & 22.)

Hoplosternum litorale is by far the commonest of the three species of *Hoplosternum* and *Callichthys* which inhabit these swamps. It is readily found at all seasons of the year anywhere in the stretch of more or less open water at the edge of the swamp. Its nest is a striking feature of this region, and we had many opportunities of observing it and the breeding-habits of the fish. We had also opportunities of collecting the young and observing their habits. We were not able to make similar observations on the breeding-habits and development of the other species. In the following account, therefore, the description of the breeding habits and development refers to *H. litorale*: that of the structure and physiology of the adult is true in general for all three species, but is derived from observations on *H. litorale*, unless the contrary is stated.

Breeding Habits.

Some account of a nest built by a pair of these fish in an aquarium in this country has been given by Vipan (1886). His description agrees closely, in the points with which he deals, with our observations of the habits of the fish in its natural environment.

The fish begin to build their nests immediately after rain in the early part of the summer (October-December). Rain at the beginning of the summer is the stimulus for the breeding of many of the fishes of these swamps (*Lepidosiren*, *Symbranchus*, *Hoplias*, etc.) and of many of the Amphibia. After the rain the water is often cooler than usual, but it rapidly heats in the following days. The amount of oxygen in the water is not greatly altered by the rain, except for a short time and at the surface. The most definite abnormality of the water at this time is the less amount of carbon dioxide in it, but this also passes off rapidly. Possibly a combination of all these changes provides the stimulus for reproduction.

The nest is made among the floating weed and other aquatic plants at the surface of the water of this part of the swamp. It consists of a raft, about 1 foot in diameter, made of the dead and dying leaves and stems of these plants. The mass of eggs is placed at the centre of the underside of this raft. The eggs are glued together and to the raft by a secretion, which also prevents the materials of the raft from falling apart. Below the eggs and covering the whole of the underside of the nest is a mass of foam, probably made by the fish by taking air in at the mouth and bubbling it out again. The nest is guarded by the parent fish, which is always to be found swimming below it, but it is readily deserted if the fish is disturbed in any way.

A function of the foam may perhaps be to keep up the oxygen content of the water surrounding the eggs and to provide the young fish, which remain in the nest for some days after hatching, with a source of oxygen for their respiration. It has been mentioned in the previous paper (Carter & Beadle, 1930 *b*)

that the development at the temperature of the surface water of the swamp is very rapid and the need for oxygen therefore great. The water surrounding the nest is often almost entirely without oxygen, and some accessory source is necessary for the development of the eggs.

The habits of the young fish after hatching were observed in tanks and dishes in the hut which served us for a laboratory. Nests in which the eggs were nearly ready to hatch were collected, and the larvæ, after hatching from the eggs, lived in the dishes for more than a week, by which time the yolk had been completely absorbed. Within a few hours of hatching, they were observed to come to the surface of the water and to make use of the surface layer for their respiration. They did not at this stage swallow air. In the natural conditions they pass the period of the absorption of yolk in the nest. The bubbles which form the foam provide them with a surface layer, which they could not otherwise get without leaving the protection of the nest.

It is possible that the foam may also serve to prevent the nest from sinking, but we found that deserted nests without foam often remained on the surface for some days. It seems that this is at most a secondary function.

A drawing of the nest in the swamp is reproduced in Pl. 20, fig. 5. The foam (*fo.*) can be seen at the edge of the nest. Another of the underside of the nest, showing the mass of eggs (*e.*), is given in Pl. 20, fig. 6.

Structure of the Adult.

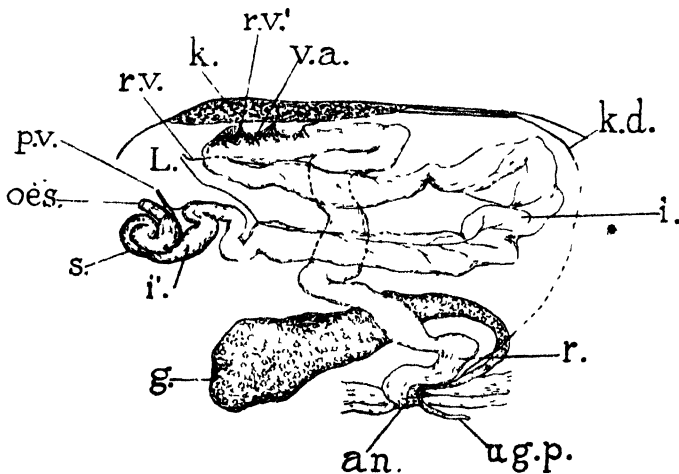
The accessory respiratory organ in all three species of these genera is the wall of the intestine from a point a very short distance behind the stomach to the rectum. The whole of this part of the intestine is normally full of air and empty of food.

Jobert (1877), in his paper on the *Callichthys* of Brazil (*C. asper*, which is given by Eigenmann (1910) as a synonym of *C. callichthys*), describes the macroscopic structure of this organ very shortly and mentions its blood-supply, but he gives no figures and few details of the histology. So far as his description goes, it agrees with that given in this paper.

In Pl. 21, fig. 9 a view of a dissection of an adult fish is given in which the left abdominal wall, the left gonad, and the greater part of the kidney on the left side have been removed. The respiratory part of the intestine (*i.*), which is thin-walled and transparent, is seen to occupy the greater part of the body-cavity. Its coils lie over one another in this figure. They pass five times up and down the cavity. Their arrangement can be more clearly seen in the drawing of text-fig. 1. In this figure the alimentary canal is shown as it appears after its coils have been unravelled and arranged as nearly as possible in their natural position. The œsophagus leads directly into a thick-walled and muscular stomach (*s.*), which is coiled upon itself. For a short distance (5 mm.) behind the stomach the intestine is of normal structure (*i.*'), but immediately behind this the wall becomes transparent (*i.*) and of the type of the whole of the rest of the intestine. The rectum (*r.*) is thick-walled and very short.

The blood supply of the intestine is shown in text-figs. 1 and 2. The right posterior cardinal vein (*p.c.v.*) opens directly from the large interrenal vein (*i.r.v.*), which is continuous through the kidney with the caudal vein (*c.v.*). Near the front end of the kidney a large vein (respiratory vein, *r.v.*) joins the interrenal vein. It is formed by several branches from the coils of the thin-walled part of the intestine. The greater part of the coils are drained by this vein, but that lying immediately below the kidney also sends a number of small veins to the interrenal vein through the substance of the kidney. This coil of the intestine is more strongly vascular than any other part.

TEXT-FIG. 1.

The alimentary canal of *Homosternum liturale*

The coils of the alimentary canal are arranged as nearly as possible in their natural position, but are somewhat spread out in order to show their arrangement. The left gonad has been removed. The respiratory part of the intestine is unshaded.

<i>an.</i>	anus	<i>as</i>	oesophagus
<i>g.</i>	gonad	<i>pt</i>	hepatic portal vein.
<i>i.</i>	respiratory intestine.	<i>r.v., r.v.'</i>	respiratory vein
<i>i'.</i>	thick-walled intestine.	<i>s.</i>	stomach
<i>k.</i>	kidney.	<i>ug.p.</i>	urinogenital papilla.
<i>k.d.</i>	kidney duct.	<i>v.a.</i>	vascular area of the intestine.
<i>L.</i>	liver.	<i>r.</i>	rectum.

The path of one of these small veins through the kidney can be seen in the transverse section shown in fig. 10, *r.v.'* (Pl. 22).

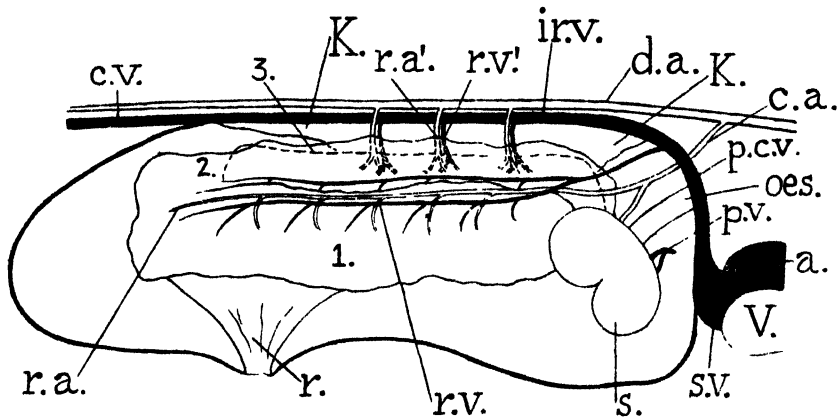
The coeliac artery (*c.a.*) leaves the dorsal aorta at the front end of the body-cavity and follows a course parallel to that of the larger respiratory vein, passing backwards among the coils of the intestine. It differs from this vein in that it also gives off branches to the stomach. It is probable that small arteries (*r.a.'*)

arise from the dorsal aorta behind the coeliac artery to supply the area of the intestine which is supplied by the smaller respiratory veins (*r.v.*'), but it was not possible to trace vessels of so small a size among the tubules of the kidney.

Histology.

The finer structure of the wall of the respiratory part of the intestine is shown in figs. 11 and 12 (Pl. 22). It will be seen that the thinness of the wall is chiefly due to the reduction of the muscle layers. The inner surface is formed by a single layer of epithelial cells (*i.ep.*), which are not greatly reduced, being

TEXT-FIG. 2.



Blood supply of the intestine in *Hoplosternum littorale*.

Lettering as in text-fig. 1, and:—

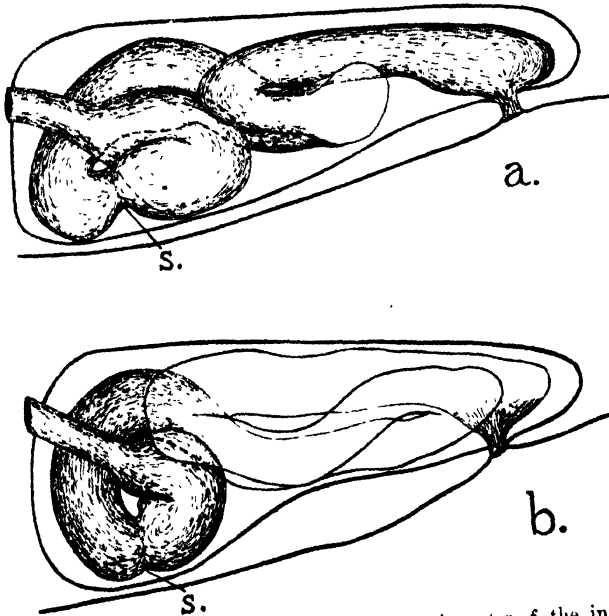
a. atrium.	r.a. respiratory artery.
c.a. coeliac artery.	r.a.' probable respiratory arteries
c.v. caudal vein.	passing through the
d.a. dorsal aorta.	kidney.
ir.v. interrenal vein.	s.v. sinus venosus.
k. kidney.	V. ventricle.
p.c.v. posterior cardinal vein.	
1 3 The first three loops of the respiratory intestine.	

about 8-10 μ in height. These cells are rectangular and unciliated. No gland cells could be found among them. Outside this epithelium are two or three layers of nuclei belonging to connective-tissue cells and to the inner layer of muscle. The remainder of the wall is formed by a layer of longitudinal muscle, 15 μ thick, and by a very thin coelomic epithelium (*c.ep.*). Numerous blood-vessels (*ve.*, Pl. 22, figs. 10-11) are to be seen on the outside of the wall, covered only by the epithelium. Smaller vessels arise from these and pass to the intestinal epithelium. Among the cells of this epithelium, capillaries arising from these

vessels are very numerous. They are about 8μ in diameter and lie in the inter-cellular spaces between the cells. They are everywhere covered on the inner side by processes of the cells (Pl. 22. fig. 12). This capillary network extends over the whole of the thin-walled part of the intestine, but it varies in density and is most dense in the coil immediately below the kidney supplied by the smaller respiratory veins.

The structure of the intestinal epithelium is strikingly similar to that of the respiratory intestine of the loach (*Misgurnus fossilis*, Calugareanu, 1907). In

TEXT-FIG. 3.



Two stages in the development of the respiratory character of the intestinal wall in *Hoplosternum litorale*: *a*, in a fish 9 mm. long; *b*, in one 22 mm. long. The respiratory part of the intestine is shown unshaded, the stomach and absorptive part of the intestine shaded.

pyloric sphincter.

both, the capillaries lie between the cells of a single-layered and unciliated epithelium, only differing in its greater height in the loach. The muscle-layers are thicker in the loach, but otherwise similar.

Development.

Two stages in the development of the intestine are shown in the drawings of reconstructions reproduced in text-fig. 3. The respiratory character of the wall first appears when the fish is 9 mm. long (*a*). It has then been hatched for a considerable time, and the yolk has long been absorbed. It has already

assumed⁷ very nearly the adult form. The first appearance of the respiratory character of the wall is at a point midway between the stomach and the anus, where a small part of the intestine becomes thin-walled. As development continues, the respiratory part of the intestine extends in both directions. When the fish is 22 mm. long (b), all that part of the intestine which is respiratory in the adult has taken on this function and the thin-walled structure. During later development, growth goes on by increase of the complexity of the intestinal coils. As soon as the wall becomes thin, its histological structure becomes very similar to that of the adult.

Behaviour and Physiology.

The wall of the intestine of this fish has been shown in the previous pages to be of a type which is very suitable to serve the purpose of respiration. It remains to show that it is used for this purpose.

It has been stated that the thin-walled intestine is always empty of food and filled only with gas. In all the specimens which we opened this was so. Food is to be found in the stomach and in the absorptive piece of the intestine behind it, and the remains of food in the rectum*.

All the three species of *Hoplosternum* and *Callichthys* which live in these swamps come to the surface at frequent intervals and breathe air. Jobert (1877) observed that the race of *C. callichthys* with which he experimented in Brazil did this, but his description of its behaviour differs in one point from that observed by us. He states that the air is passed through the alimentary canal and voided at the anus. In the fishes which we examined, the air is always passed out at the mouth or at the gill opening. This is true of *C. callichthys* as of the other two species. It is possible that the behaviour of the race of this species in Brazil differs from that of the fish in these swamps.

It is easy to show that the fish depends upon the air taken in at the mouth for its respiration. It is to be found in the swamp at all times of the year, and often in water which is rapidly drying and very foul. It sometimes travels over the grassland from one pool to another, especially at dawn, when the grass is wet with dew. Definite proof that this air is necessary for the fish is given by the observation that it can be drowned by being prevented from reaching the surface of the water in which it is living, however well oxygenated

* In some way the food must be passed down this long and weak intestine, but it is by no means clear how this is done. Ciliary propulsion is excluded by the absence of cilia on the wall of the intestine, and the thinness of the muscle layer makes it improbable that it is driven by peristaltic movement, even at unfrequent intervals. Contractions of the body-wall could not move the food along the complex windings of the intestine. The only suggestion which it seems possible to make is that the intestine is occasionally contracted and emptied of air (it would seem probable that the thin muscle layers would be competent to do this), and that the food, which consists of soft vegetable matter, is rapidly passed down by pressure from behind. Possibly it may be partly driven by peristalsis in this contracted condition.

the water is. Jobert found that *C. callichthys* died under these conditions in a tank; but a small quantity of water in which a fish is living soon becomes deoxygenated, and this experiment does not prove that the fish is unable to live by aquatic respiration in well oxygenated water. We were able to show that it cannot do so by experiments in which the fish was placed in the tank provided with a spray of water on its surface (p. 336), and prevented from taking air by wire netting. It died in $2\frac{1}{2}$ hours. It has been stated that the water was always well oxygenated in this tank. The fish can live indefinitely in water containing as little as 0.2 c.c. per litre of oxygen, if it is allowed to reach the surface. That the gills are not functionless is shown by the observation that the movements of the gill-chamber increase both in frequency and extent when the fish is prevented from taking air and is becoming stifled.

The degenerate structure of the secondary folds on the gill-lamellae of this fish has been noted above (p. 339).

It can also be shown that the air which is taken in at the mouth is passed to the intestine. When it is given out at the anus, as happens, according to Jobert (1877) in the Brazilian race of *C. callichthys*, it is clear that it passes through the intestine, but in our observations it escaped at the mouth or at the gill-opening, and proof is then needed that it is not retained in the pharynx or gill-chamber. In this connection the result of an experiment similar to that on *Erythrinus*, previously described, was definite. We opened the body-cavity of a living fish by removing parts of two of the large scutes which cover the sides of the body, and cutting the muscles below them. The intestine was pierced and the cut held open by a prop. When the fish was returned to the tank, it showed no more disturbance than did *Erythrinus* in similar circumstances, and lived for many hours. On each occasion on which it came to the surface and swallowed air, bubbles of gas escaped at the puncture in the intestine. The disturbance was indeed less than in *Erythrinus* for there was no increase in the frequency of the visits to the surface.

This experiment can leave little doubt that the swallowed air is passed to the intestine. Since the respiration depends upon this air, it is difficult to avoid the conclusion that the intestine is used as an accessory respiratory organ. In order to confirm this conclusion, the gases of the intestine were analysed. Jobert (1877) made analyses of the gas voided by the anus by his specimens of *C. callichthys*, and found 1.5–3.8 per cent. of carbon dioxide and "an excess of nitrogen." But he states that the results were very variable, and gives no details of his method of analysis, except that it was by means of potassium hydrate and pyrogallie acid. The early date of these analyses (1877), and the fact that the danger of error due to solution of the gases during prolonged contact with water was not always avoided at the time, makes it impossible to accept these results without question.

Our analyses were made by the method described in the section of this paper on *Erythrinus* (p. 331). When an analysis of gas from a fish respiring normally was to be made, the gas was collected, as described there, immediately after

the fish had been killed by a blow upon the head. Six analyses of this type gave percentages of oxygen varying from 9.6 to 20 and an average of 15.9. A measurable amount of carbon dioxide was found in only one of these analyses, and the percentage was then 1.3. The gas is therefore much closer in composition to atmospheric air than that of the air bladder of *Erythrinus*, but it shows a significant reduction in the percentage of oxygen. Since the gas is continually renewed from the atmosphere, this result shows that there is a considerable absorption of oxygen in the intestine.

The difference between the gas and air should be greater in fish which have not been allowed to renew the gas. Analyses of gas from fish which were on the point of death in tanks in which they could not reach the surface were made. In only one of three such analyses was a measurable percentage of oxygen found, and it was then 3.4 per cent. The average percentage of carbon dioxide was 3.2. These results therefore confirm the conclusion that there is a considerable absorption of oxygen in the intestine, and they show that some carbon dioxide is excreted.

LORICARIIDÆ.

ANCISTRUS ANISITSI Eigenmann & Kennedy. (Pl. 23.)

In this fish the large U-shaped stomach is always full of gas during life, and was found on investigation to be used as an accessory respiratory organ. It appears that aerial respiration has not previously been noted in this genus. Jobert (1878, p. 2) refers to this habit in a species of the old genus *Hypostomus*, which he does not further define. Species of *Ancistrus* were included in this genus by Cuvier and Valenciennes (1837) and other authors, but it is clear that the fish to which he refers is not that described here. In his species the accessory respiratory organ is "a small part of the intestine immediately behind the stomach"; in *Ancistrus anisitsi* the stomach itself is respiratory.

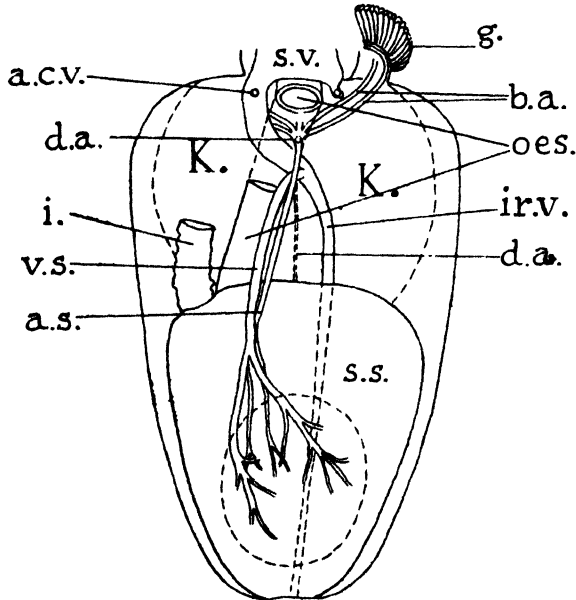
This is a comparatively rare fish in the swamps of the Chaco. Only five examples of the adult were brought to us during the nine months of our visit. In spite of this the eggs are sometimes taken by the Indians, who use them for food. We had opportunities of collecting them, and the young fish were often caught in nets among the floating weed of the outer part of the swamp. The eggs are laid in holes in banks at the edge of the swamp and are glued together by a secretion. They were found to live well in dishes, and the larvæ which hatched from them were kept alive for 7-10 days. By this time the yolk-sac had been completely absorbed, and it is probable that the larvæ died from starvation.

By means of material collected in these ways we were able to study the development through all its stages up to that at which the young fish was 40 mm. long, and its structure was nearly that of the adult. Owing to the position of the nest, always under water and in a dark hole, we were not able to observe the breeding-habits of this fish.

Structure of the Adult.

When the ventral wall of the body-cavity is removed, the very numerous coils of the intestine are seen forming a thick pad which occupies the whole of the ventral part of the cavity (c.i., fig. 14. *a*, Pl. 23). The arrangement of the remaining organs after this pad and the gonad have been dissected away is shown in fig. 14, *b*. The œsophagus (*œs.*) enters the cavity among the lobes of the liver, passes backwards for about one-third of the length of the cavity, and then appears to leave it and enter the dorsal part of the body. If

TEXT-FIG. 4

Blood supply of the stomach in *Ancistrus ansata*. Ventral view.

<i>a.c.v.</i>	opening of the anterior cardinal vein.	<i>ir.v.</i>	interrenal vein
<i>a.s.</i>	artery to the stomach sac.	<i>K.</i>	kidney.
<i>b.a.</i>	efferent branchial arteries.	<i>œs.</i>	œsophagus.
<i>d.a.</i>	dorsal aorta.	<i>s.s.</i>	stomach sac.
<i>g.</i>	gills.	<i>s.v.</i>	sinus venosus.
<i>i.</i>	intestine.	<i>v.s.</i>	vein from stomach sac

its course is followed at the point at which it disappears, it is found to enter a shallow sac (*s.s.*), separated from the rest of the cavity by a thick membrane, which passes insensibly at its edges into the peritoneum. This membrane is tendinous and opaque except in a central circular area (*t.a.*), about 1 inch in diameter in a fish 12–15 inches in length. In this area the wall of the sac is very transparent, and many blood-vessels can be seen through it.

Within the sac the oesophagus widens into a U-shaped stomach, which is attached to the wall of the sac in the transparent area, but is free elsewhere. A view of this stomach, as it is seen after the membrane has been cut through round its edges and turned over so as to show its inner surface, is given in fig. 14, c (Pl. 23).

The wall of the stomach is very thin and transparent, and is vascular in all parts. It is the blood-vessels of the stomach wall which are seen from the outside through the transparent area in the ventral wall of the sac. The stomach wall is also very contractile. Usually it is shrivelled in preserved material by contraction of its muscles, and the stomach then occupies only a small part of the cavity of the sac, but in life it is extended and fills the whole of the cavity. This is occasionally so in preserved material.

The posterior arm of the stomach reaches the wall of the sac at its front end on the right side, and here the sphincter is situated. It opens into a wide intestine outside the sac. This passes to the left side of the body, dorsal to the oesophagus, and at once turns ventrally, rapidly narrowing, to join the coils of the hinder part of the intestine.

There is no trace of an air bladder in the body-cavity, either in the adult or in the larva at any stage of its development after it is hatched.

The blood supply of the stomach is shown in text-fig. 4. The arterial supply comes from the aorta by the coeliac artery (*a.s.*). This artery leaves the aorta immediately behind the point at which the most posterior efferent branchial arteries join it, and runs back along the oesophagus to the stomach. It is very large and much of the blood in the aorta must pass along it. Inside the stomach-sac it can be traced on to the wall of the stomach, and can be seen to break up into very numerous vessels on the wall.

The veins from the stomach join the interrenal vein (*ir.v.*). The right posterior cardinal vein alone reaches the dorsal side of the body-cavity and is continuous through the kidney with the interrenal vein, which lies somewhat to the left side of the body. Near the front end of the body-cavity a large vein (*v.s.*) joins the interrenal vein. This vein can be traced backwards alongside the coeliac artery into the sac. With the artery its further course can be traced on to the wall of the stomach, where it is formed by the fusion of many smaller vessels.

Histology.

The thin wall of the stomach has a structure very similar to that of the intestines of *Hoplosternum* and *Misgurnus*. A section through a small piece of the wall is shown in fig. 13 (Pl. 22). This figure was drawn from a section of the wall in a larva 30 mm. long. In the adult the wall is thicker (100 μ), but is otherwise very similar in structure. In both the larva and the adult the muscle layers are less reduced than in the other respiratory organs of the alimentary canal.

The inner surface of the wall is formed by a single layer of cubical and unciliated epithelial cells (*ep.*), which are about 10μ in height. The capillaries lie in the intercellular spaces between these cells. They are always covered by processes of the cells. No gland cells could be found in the epithelium.

The arrangement of the muscle layers is similar to that of the muscles in the intestinal wall of *Hoplosternum*. There is a thin ectonic epithelium, below which the larger blood-vessels lie (not shown in the figure). Smaller vessels (*ve.*) can be seen passing through the muscle layers towards the capillaries in the epithelium. The capillary network extends over the whole of the wall of the stomach and is everywhere dense.

Development.

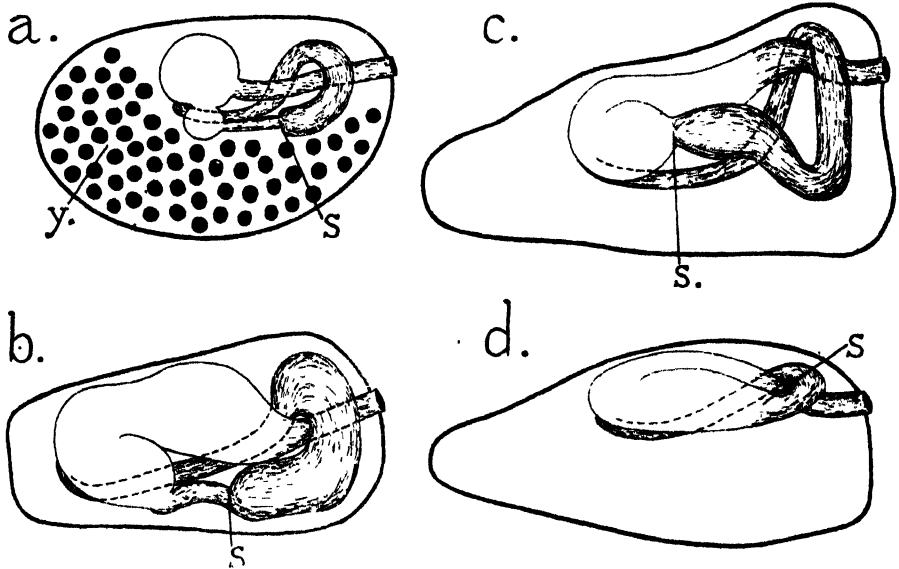
The diagrams of text-fig. 5 represent four stages in the development of the respiratory character of the wall of the stomach of this fish. When the larva hatches from the egg, part of the stomach has already developed a thin and transparent wall (*a*), and the histological structure is already similar to that of the wall of the adult. A large part of the stomach in front of the sphincter has still a thick and absorptive wall. The oesophagus also stretches much further back than in the adult. As a result, both arms of the respiratory organ are short, and it is not U-shaped, as it is in the adult, but has the form of two spherical vesicles, of which one is much smaller than the other. The respiratory character of the wall at this time is associated with the simultaneous development of the habit of breathing air (see below, p. 352).

The growth of the anterior arm of the respiratory organ is much more rapid than that of the posterior. It is complete when the yolk has been absorbed (*b*). The respiratory character of the wall does not reach the sphincter until the larva is 2.5–3.0 mm. long (*c*).

During the development great changes occur in the relative sizes of the different parts of the alimentary canal. When the larva hatches, the hinder part of the intestine consists of five or six coils, and these are arranged around the stomach on the dorsal side of the yolk. As development goes on, this part of the intestine becomes continuously longer and the coils more numerous. They also move ventrally until they form in the adult the large pad mentioned above. In the earlier stages the first coil behind the sphincter is very large (5 *a*, *b*, *c*). It is at its maximum size, compared with the body cavity, when the larva has just absorbed its yolk (5, *b*). It decreases thereafter continuously. But the most striking change is the relative decrease in the size of the stomach in the later stages of development. In text-fig. 5, *b* it occupies at least one-half of the body cavity. As the larva grows, it shrinks more and more towards the dorsal side, making room for the increasing number of the coils of the intestine. In the adult it does not occupy more than one-tenth of the space of the cavity. The decrease in its size is especially rapid when the young fish is growing from 30–40 mm. The whole development suggests that the first

coil of the intestine has an important digestive function in the young larva, which is later taken over by the hinder part ; and, possibly, that the respiratory function of the stomach is at its maximum of utility in the larva in which the yolk has just been absorbed. The evidence to be given below indicates that at least some part of the respiration is carried on by it in the adult. It therefore functions at all stages of the life-history after the larva is hatched.

TEXT-FIG. 5.



Development of the respiratory stomach of *Ancistrus anisitsi*.

Four views of the respiratory stomach and anterior part of the intestine from the right side. From reconstructions of serial sections. The respiratory part of the stomach is shown unshaded. Diagrams not to scale.

- (a) The stage of development at hatching, 11 mm.
 - (b) At the end of the period of absorption of the yolk, 14 mm.
 - (c) In a young fish, 25 mm. long.
 - (d) " " " 40 " "
- s pyloric sphincter. y. yolk.

Behaviour and Physiology.

The fish breaks the surface and swallows air at irregular intervals. The expired air is given out at the mouth. Larvæ which had been hatched in captivity came to the surface immediately after they had escaped from the egg, and at once began to swallow air. In the abdomen the bubble of air filling the thin-walled part of the stomach can be seen at this and later stages. There can therefore be no doubt that in these larvæ the air is passed to the stomach. In this respect the larvæ differ from those of *Hoplosternum*, which do not swallow

air until a much later stage. In both fish the accessory respiratory organs function as soon as they have attained the appropriate structure. The larva can live for twenty-four hours, and probably indefinitely, in well oxygenated water in which they are unable to reach the surface. They die if the water is not well oxygenated. The respiration carried on by the gills is therefore sufficient to maintain life only if the water is well oxygenated.

Owing to the small number of specimens of the adult which we were able to collect—and they were not all in a healthy condition when they were brought to us,—it was not possible to perform many experiments on the adult fish. Only two analyses of the gases of the stomach were obtained. In both these analyses no measurable amount of carbon dioxide was found, but the percentage of oxygen was decidedly less than that in air (15.7 and 11.8 per cent.). Since the larva certainly passes the air taken in at the mouth to its stomach, and the adult also swallows air, it can hardly be doubted that it is passed to the stomach in the adult also: and, if this is so, and the gas in the stomach is therefore continually renewed, these analyses give evidence that absorption of oxygen takes place there. In conjunction with the evidence of the respiratory character of the structure of the wall of the stomach—and especially of its similarity to that of the wall of the intestine of *Hoplosternum*, the respiratory function of which the evidence, which has been given, will, it is hoped, establish—the results of these analyses leave little doubt that the stomach of *Ancistrus anisitsi* is also respiratory.

DISCUSSION.

(1) *Adaptations to Aerial Respiration in the Fishes.*

The habit of supplementing the respiration of the gills by aerial respiration, carried on in one part or another of the body, occurs in very many fishes besides those described in this paper. The list is a long one, if only those fishes are included which possess an organ which has been shown on good evidence to have the function of aerial respiration. It would be much longer if all the fishes were added in which some author has believed that aerial respiration occurs. In preparing the following table (pp. 354-355) a selection has been made; only those fishes are referred to which can be said without much doubt to breathe air to some extent. The selection was carried out on the criteria that, if the organ is to be accepted as one of aerial respiration, it must be shown:

- (1) That air is passed in and out of the organ:
- (2) that a capillary network is present.

The satisfactory proof of these two points does not establish the respiratory function of the organ completely, but, in the absence in most cases of experiments on the physiology of the organ, it makes it very probable that it is used for this purpose.

TABLE I.

Accessory Respiratory Organs in the Fishes.

Type of Accessory Organ.	Family and Species	Circulation.		Habitat.	Author*
		Afferent.	Efferent.		
I. Pharyngeal diverticula.					
	OPHIOCEPHALIDÆ. <i>Ophiocephalus</i> spp.	Aortic arches, III, IV.	Jugular vein.	Tropical pools etc., Asia, Africa.	Rauther (1910). Das (1927).
	GONIDÆ. <i>Periophthalmus Kolbentri</i> .	Carotid artery.	Jugular vein.	Muddy tropical shores.	Rauther (1910).
II. Diverticula of the branchial chamber.					
	CLARIIDÆ. <i>Clarias magur</i> .	Afferent arches.	Efferent arches.	Tropical pools, India, etc.	Rauther (1910). Das (1927).
	<i>Succobranchius fossilis</i> .	Afferent arches.	Efferent arches.	Tropical pools, India, etc.	Rauther (1910). Das (1927).
	ANABANTIDÆ. <i>Anabas scandens</i> .	Efferent arches.	Jugular vein.	Tropical pools, India, etc.	Rauther (1910). Das (1927).
	<i>Macropodus opercularis</i> .	Efferent arches.	Jugular vein	Tropical pools, India, etc.	Rauther (1910). Das (1927).
	<i>Osphremenus</i> spp.	Efferent arches.	Jugular vein.	Fresh waters, S. Asia.	Rauther (1910). Das (1927).
	<i>Betta pugnax</i> .	Efferent arches.	Jugular vein.	Fresh waters, S.E. Asia.	Rauther (1910). Das (1927).
	AMPHITRIDIDÆ. <i>Amphitritus cuchia</i> .	Aortic arches, III, IV.	Jugular vein.	Rivers etc., India, Burma.	Rauther (1910). Das (1927).
III. Branchial chamber filled with air.					
	STERNARCHIDÆ. <i>Hypopomus brevirostris</i> .	Afferent arches.	Efferent arches.	Swamps of S. America.	This paper.
	SYMBRANCHIDÆ <i>Symbranchus marmoratus</i> †.	Afferent arches.	Efferent arches.	Swamps of S. America.	Dareste (1873). Taylor (1913).
IV. Epithelium of pharynx respiratory.					
	SYMBRANCHIDÆ. <i>Monopterus javanensis</i> .	Aortic arches.	Jugular vein.	Fresh waters, S.E. Asia.	Das (1927).

V. *Air bladder and lung.*

POLYPTERIDÆ. <i>Polypterus</i> spp.	Eff. arch, VI.	Hepatic vein.	Rivers, swamps, Africa.	Budgett (1900, 1901 <i>a</i> , <i>b</i>). (Graham-Kerr (1907).
AMIIDÆ. <i>Amia calva</i> .	Dorsal aorta.	R. post. card. vein.	Rivers, N. America.	Wilder (1886)
LEPIDOSTEIDÆ. <i>Lepidosteus</i> spp.	Dorsal aorta.	R. post. card. vein.	Rivers, N. America.	Potter (1927).
OSTEOGLOSSIDÆ. <i>Arapaima gigas</i> .	Renal and inter- costal arteries.	Card. and inter- costal veins.	Swamps, N. America.	Jobert (1878).
MORMYRIDÆ. <i>Gymnarchus niloticus</i> .	Aortic arches, V, VI.	Direct vein to atrium.	African rivers and swamps.	Budgett (1900). Asheton (1907).
CHARACINIDÆ. <i>Erythrinus</i> spp.	Coeliac artery.	R. post. card. vein.	Swamps, S. America.	Jobert (1878). This paper.
ESOCIDÆ. <i>Imbra krameri</i> .	Coeliac artery.	R. post. card. vein.	Stagnant waters, Europe.	Rauther (1914).
DIPNOI. <i>Lepidosiren paradoxa</i> .	Aortic arch, VI.	Pulm. vein to L. auricle.	Swamps, S. America.	Robertson (1913).
<i>Neoceratodus forsteri</i> .	Aortic arch, VI.	Pulm. vein to L. auricle.	Australian rivers.	Spencer (1892).
<i>Protopterus</i> spp.	Aorti arch, VI.	Pulm. vein to L. auricle.	African rivers and swamps.	Budgett (1900). Parker (1892).
VI. <i>Stomach and intestine.</i>				
CORIIDÆ. <i>Migurnus fossilis</i> , and other genera and species.	Dorsal aorta.	Portal vein.	Temp. and trop. rivers and pools.	Calugareanu (1907).
DORADIDÆ. <i>Doras</i> spp.	S. American swamps and rivers.	Jobert (1878).
CALlichthyidÆ. <i>Callichthys</i> spp.	Dorsal aorta.	Interrenal vein.	S. American swamps.	Jobert (1877). This paper.
<i>Hoplosternum</i> spp.	Dorsal aorta.	Interrenal vein.	S. American swamps.	This paper.
LORICARIIDÆ. <i>Ancistrus unisiki</i> . <i>Hypostomus</i> sp.	Coeliac artery.	Interrenal vein.	S. American swamps. S. American swamps.	This paper. Jobert (1878).

* Only the most recent or general papers on each species are given in this column.

† This fish should also be included in categories IV and I.

It will be seen that the accessory respiratory organs are very diverse. They are grouped into six categories in the table, but this classification merely groups together the organs occurring in the same part of the body, and is not intended to imply any phylogenetic connection between the various organs in each group. In fact, there is in general no such connection. Almost every species included in the table is either so distantly related to all the rest, or so differently adapted, that the adaptations must be considered to have been separately evolved in almost every case.

Further, the respiratory function is almost always new. Only the air-bladder and its equivalent, the lung of the Dipnoi, can possibly be regarded as organs which were originally respiratory, retaining that function to varying extents in different fishes. That the respiratory function of the air-bladder is a persistence of the previous general use of the organ for this purpose is exceedingly doubtful, and even here the details of structure are sufficiently different to show that the peculiar adaptations of each form have been evolved along separate lines.

These adaptations are all reactions in a single group of animals to the same physiological need. It is therefore not surprising that certain common characteristics can be traced through the structure and physiology of the whole series, and it seems probable that a consideration of these similarities may throw light on the differences between aquatic and aerial respiration in the economy of the animal. Their number and diversity make them excellent material for the study of such a subject.

In the following pages some of these points of similarity are discussed.

(a) *The Respiratory Function of the Accessory Organs.*

In these fishes the accessory respiratory organ is not the only organ of respiration. They all possess gills, sometimes reduced, but only in comparatively few species, and always apparently capable of functioning. It is also probable that the skin plays some part in the respiration of the body (*cf.* Calugareanu, 1907; Krogh, 1904), and the epithelium of parts of the alimentary canal may also do so. These are all organs of aquatic respiration. So long as the fish remains in the water (and most of them do not frequently leave it), these organs will function as such, so far as they are allowed by the nature of the water to do so; and, when it leaves the water, they probably act as lungs, perhaps inefficiently. We have therefore to consider how the functions of these different organs relate to one another in co-operating towards the total respiration of the animal.

To approach this question the most direct method would be to collect separate data of the results of the functioning of the organs of aquatic and aerial respiration, when both types are functioning at the same time. To collect such data would be difficult. It would mean that the fish must be enclosed in large vessels of water, but with access to the air, in order that both types of respiration

might be carried on, and that both the water and the air must be analysed. Even so, such experiments would not be accurate, owing to the diffusion of the gases between the air and the water.

TABLE II.

Analyses of the Gases of the Air-Bladder and other Respiratory Organs of Fish from the Swamps of the Paraguayan Chaco.

		No of experi- ments.	Average composition of the gas.	
			O ₂ (per cent.).	CO ₂ (per cent.).
A. Air-breathing fishes.				
Physostomi.				
CHARACINIDÆ.				
<i>Erythrinus unitaenatus.</i>	Air-bladder.			
	Normal	5	7.7	0.7
	Suffocated	3	1.8	1.5
CALLICHTHYIDÆ.				
<i>Hoplosternum litorale.</i>	Intestine.			
	Normal	6	15.9	.2
	Suffocated	3	3.4	3.2
LORICARIDÆ.				
<i>Ancistrus anisitsi.</i>	Stomach			
	Normal	2	13.8	0
B. Non-air-breathing fishes.				
Physostomi.				
CHARACINIDÆ.				
<i>Pyrchobius australis.</i>	Air-bladder.			
	Normal	5	5.8	1.1
<i>Tetragonopterus</i> sp.	Air-bladder.			
	Normal	2	5.2	0
<i>Hoplias [= Macrodon] malabaricus.</i>	Air-bladder			
	Normal	6	3.3	1.9
SILURIDÆ.				
<i>Rhamdia quelen.</i>	Air-bladder.			
	Normal	1	6.0	0.7
<i>Trachycoristes striatulus.</i>	Air-bladder.			
	Normal	2	9.7	0
Physoclisti.				
CICHLIDÆ.				
<i>Acara portalegrensis.</i>	Air-bladder.			
	Normal	3	34.0*	2.2

These difficulties can be avoided if it is assumed that the respiratory quotient cannot differ very far from unity †. With this assumption, approximate comparisons of the respiration carried out in the two types of organ can be obtained

* Very variable (20-50 per cent.).

† Its true value is probably in the neighbourhood of 0.7 (Winterstein, 1921). It will be seen that a deviation from unity of this amount will not affect the conclusions reached in the argument of the following pages.

from analyses of the results of only one of them. In particular, their relative effectiveness in the two main respiratory exchanges, the absorption of oxygen and the excretion of carbon dioxide, can be compared. Something can therefore be learnt on these points from the analyses of gases from the organs of aerial respiration given in the preceding pages. These results are summarised in Table II. (p. 357). With them are placed for comparison the results of some analyses of gases from the air bladders of fish which do not breathe air*.

It will be noted that a higher percentage of oxygen is normally found in the accessory organ than in the air-bladder of those fishes living in these swamps whose respiration is purely aquatic. It has been remarked above that this is not surprising, if the accessory organ is used as an organ of respiration. The gas in it is renewed from the air, whereas that in the air-bladder of other fish presumably is not.

Allowing for possible under-estimation of carbon dioxide owing to solution of the gas in the water during the analysis (see p. 336, above), these results are in fair agreement with the few comparable results which have been published by previous authors. Rarely as much as 3 per cent. of carbon dioxide is found in the gas of the respiratory organ. In Table III. the results of previous authors are collected.

TABLE III.

	Average composition of gas.		Author.
	O ₂ , per cent.	CO ₂ , per cent.	
<i>Lepidosteus</i> sp. Air bladder	3.79	2.44	Potter (1927).
<i>Erythrinus unitaeniatus</i> . Air bladder	—	1.3-2.4	Jobert (1878).
<i>Callichthys callichthys</i> . Intestine	—	1.5-3.8	„ (1877).
“ <i>Hypostomus</i> sp.” Intestine	—	1.5	„ (1878).
<i>Misgurnus fossilis</i> . Intestine	15.73	3.04	Calugareanu (1907).

The composition of the gas in these organs thus differs greatly from that of the alveolar air of the lungs of mammals. In man the alveolar air contains 14.5-16 per cent. of oxygen and 4.5-6.0 per cent. of carbon dioxide. Atmospheric air contains 21 per cent. of oxygen and .03 per cent. of carbon dioxide.

* It is not intended to imply that some of these fish may not occasionally pass air into the bladder in order to right their hydrostatic equilibrium. We have no evidence on this point (*cf.* Evans & Damant, 1928).

The similarity between the analyses (given in Table II.) of the gas from the respiratory organs of suffocated air-breathing fishes and from the bladders of the non-air-breathing fishes of these swamps may be due to both being in equilibrium with the blood.

The results show a marked contrast between the gases of the bladders of the physostomatous fish and that from the single physoclystic fish found in the swamps of the Chaco.

Thus in the lung the absorption of oxygen is approximately equal to the excretion of carbon dioxide: in most of the accessory respiratory organs of fishes it is at least five times as great, and in the intestine of *Misgurnus*, in which the two exchanges are most nearly equal, it is still almost twice as great. No possible deviation of the quotient from unity could account for differences as great as these in the amounts of the two exchanges. It is clear that the greater part of the excretion of carbon dioxide must be carried on elsewhere in the body, presumably mainly in the gills, and that the accessory respiratory organs are chiefly organs of oxygen absorption. Calugareanu (1907) came to this conclusion with regard to the intestine of *Misgurnus*. The results of these analyses show that it is true to a still greater extent of the accessory organs of many other fish.

The conclusion will be reached in the following pages that these organs are adaptations to life in a medium poor in oxygen rather than to migration out of the water. If this is so, it is not difficult to explain how this separation of the two respiratory exchanges has come about. The water of these swamps, and presumably of many other similar tropical waters, contains much carbon dioxide, but this gas is so soluble that saturation (over 500 c.c. per litre) is never approached. The organs of aquatic respiration are therefore always competent to carry out the excretion of carbon dioxide, whereas they are made ineffectual in the absorption of oxygen by the absence of the gas in the water. The physiological need to which the fish has to respond is therefore a need for more absorption of oxygen, and not for a general increase in the respiration. If a new organ mainly concerned with the absorption of oxygen can be evolved, and the gills retained for the excretion of carbon dioxide, this need will be satisfied.

If the new respiratory organ is one of aerial respiration, it necessarily becomes mainly an organ of oxygen absorption on account of the greater efficiency of aquatic respiration. Respiration is at base always aquatic whether it is carried out in lungs or gills, the true difference lying in the manner in which the water near the respiratory epithelium is purified; in the lung, by diffusion into the air from the thin layer covering the epithelium, in the gill, by exchange with fresh water brought near the epithelium by the respiratory current. Diffusion will only begin to be effective when a gradient of oxygen has been set up; and thus in the lung the water near the epithelium must always be far from saturated with oxygen. Further diffusion is slow, even across thin films, whereas the respiratory current will replace the water with perfectly fresh water in a small fraction of a second. The gill is therefore the far more efficient organ; and this is probably true, so far as the excretion of carbon dioxide is concerned, even in the water of the tropical swamp, although it contains much of the gas*. When the fish possesses two organs of carbon dioxide excretion, one aquatic and the other aerial, the greater part of the excretion will be carried out in the organ of aquatic respiration for these reasons. On the other hand,

* Cf. Carter, G. S., Biol. Rev. vi, 1930.

since the water is almost completely without oxygen, practically all the absorption of oxygen must go on in these fishes in the organ of aerial respiration. This organ therefore becomes mainly an organ of oxygen absorption*.

When the fish leaves the water, the organs of aquatic respiration, if they function at all, must do so as lungs. The excretion of carbon dioxide will then be carried out by all the respiratory organs, and perhaps by others than the gills and the known accessory respiratory organs. In the eel it has been shown that the skin is the seat of a large part of the excretion of carbon dioxide, when the fish leaves the water (Krogh, 1904).

(b) *The Gills as Organs of Aerial Respiration.*

It is strikingly rarely that the gills are themselves modified to be organs of aerial respiration. This occurs in *Hypopomus brevirostris* and probably in *Symbranchus marmoratus*, but not, so far as is known, in other fishes.

The inefficiency of aerial respiration compared with aquatic is true of respiration in general, and not only of the excretion of carbon dioxide. It would therefore seem that an increase of the area of the respiratory epithelium is necessary, if the gills are to serve as organs of aerial respiration and to satisfy the total respiratory needs of the body. We have seen that the secondary folds are exceptionally well developed in *Hypopomus* and *Symbranchus*, and that the gill chamber in *Hypopomus* is exceptionally large (p. 340, above). The fact that these modifications occur in these two fishes confirms the general theory†.

Probably these considerations point to one reason for the rapid death of most fishes when they are taken out of the water. It is usually believed that this is due to the structure of the secondary folds, which are admirably adapted for respiration in the water, where they stand apart, but which fall against each other and cease to function so efficiently when the chamber is emptied of water. There can be little doubt that this is in part the cause of the death of the fish, but the fact that the folds are unusually long in *Hypopomus* and yet function as organs of aerial respiration shows that this suggestion does not contain the whole truth. Even if the gills were as efficient in the air as in the water, it could not be expected that the fish would be able to live in the air.

That the gills are not more frequently adapted as organs of aerial respiration by increase of the area of the respiratory epithelium is perhaps due to the greater efficiency of aquatic respiration in the excretion of carbon dioxide. This advantage is lost by the fish when the gills are adapted to the breathing

* Krogh (Skand. Arch. Physiol. xv, 328, 1904) has shown that in the frog the greater part of the excretion of carbon dioxide takes place in the skin and the absorption of oxygen in the lung. In his experiments the respiratory quotient of the cutaneous respiration was 1.7-3.0 and that of the lung 0.3-0.57.

† It may be remarked that both these fishes are eel-like in form. It has been mentioned above that a large part of the respiration goes on in the skin of the eel when the fish is out of the water, and it is possible that a large area of the skin in *Hypopomus* and *Symbranchus* gives it a similarly important respiratory function.

of air. It is also true that the evolution of another organ of aerial respiration, mainly concerned in the absorption of oxygen, causes no change in the original method of the excretion of carbon dioxide. The principle of economy of change is therefore in opposition to the alteration of the function of the gills.

(c) *The Blood Supply of the Accessory Respiratory Organs.*

Certain common features of the blood supply of these organs can be traced through the whole series of the fishes which possess them.

The arterial supply of the organ is, as a rule, not of great interest from this point of view. The accessory respiratory organs in the body cavity are generally supplied by the coeliac artery, and those in the front part of the body from the branchial arches. In some cases the special type of arterial supply exemplified by the pulmonary arteries to the air bladder from the branchial arches in *Lepidosteus* and *Amia*, and that to the lung in the Dipnoi, is present. The arteries do not, however, show any distinctive common features.

The veins from these organs are more interesting. If the organ is on the direct course of the branchial circulation (as in *Hypopomus*, *Clarias*, *Saccolabrus*, etc.) it is to be expected that no modification of either the main venous or arterial circulation would occur. This is so. The aerated blood passes to the body by the dorsal aorta as in a normal fish, and the venous blood is brought to the organ by the afferent branchial arteries. When the organ is in some other part of the body, the most striking characteristic of the venous circulation is that the blood never passes through capillaries on its way from the organ to the heart. If the vein which carries the blood is the jugular vein, this is so without modification of the circulation: but, when the organ lies in the body-cavity, the blood would in most cases pass through the capillaries of the liver or the kidney if the circulation was unmodified. It does so only in *Misgurnus fossilis*, in which fish the blood from the intestine is carried to the heart by the hepatic portal vein. It is possible that even here there is some modification, such as a direct course for this blood through the liver, but, if so, it does not appear to have been described. No other accessory respiratory organ is drained by a vein passing into the liver, although this is the usual course for the blood from the alimentary canal to the heart, and the air-bladder is also often drained in this manner. The blood from these organs always passes into the posterior cardinal veins, except in the Dipnoi and in *Gymnarchus*, in which a separate pulmonary vein to the atrium has been evolved, and in *Polypterus*, in which the vein from the air-bladder opens into the hepatic vein between the heart and the liver. Where the vein from the organ does not open into the cardinal vein directly (as it does, for example, in *Lepidosteus* and *Amia*), the presence of capillaries in the kidney on the way to the cardinal vein is avoided by the formation of a direct vein (the interrenal) between the caudal and the posterior cardinal, and the opening of these veins into it (*Siluridæ*, *Characinidæ*, etc.).

The value to the fish of this direct course for the blood to the heart is not so clear as it seems at first sight. The veins bearing blood from the respiratory organs also bring back blood from other parts of the body. The blood in them is therefore mixed, and any capillaries on their course to the heart would not receive purely arterial blood. The blood which they received would, however, be more highly oxygenated than that in the general circulation of the body, and this may have been one reason for the adaptations which avoid their presence on the course of the blood to the heart.

Perhaps a more cogent cause of these adaptations has been the reduction, which the presence of capillaries in the vein would produce, in the pull set up by the heart on the circulation of the organ. The efficiency of the circulation in the organ would be reduced, since the movement of the blood in it would depend almost entirely on the positive pressure in the arteries and hardly at all on the pull exerted by the heart on the blood in the veins*. Capillaries should not therefore be expected on the course of the venous blood to the heart from any organ in which a particularly efficient circulation is required; and this is so in a respiratory organ.

In all these fishes, except in those in which a separate pulmonary vein has been developed, the blood is mixed everywhere in the general circulation. Its average oxygenation is kept up by the continual addition of oxygenated blood from the respiratory organ. That this is less efficient than the more usual vertebrate system, in which the tissues receive purely arterial blood, is made very obvious by the elaborate adaptations which have taken place in many vertebrates for the separation of the two types of blood. In this respect these fishes must be regarded as imperfectly adapted to the new conditions.

In the Dipnoi, and incipiently in *Gymnarchus* (Assheton, 1907), the development of the pulmonary vein is associated with the formation of septa in the heart. This is an obvious step towards the separation of the two types of blood, when these arrive at the heart by different paths, but the formation of septa would be of no value so long as the blood is mixed in the veins. The formation of a pulmonary vein is clearly the first step in the separation of the two types of blood. The division of the heart is not to be expected in fishes which possess accessory respiratory organs, unless a pulmonary vein has already been developed.

(2) *Air-breathing in the Fishes in relation to their Environment.*

The series of papers to which this belongs is concerned mainly with the biometrics of the tropical swamp. From this point of view, the most remarkable feature of the adaptations of fishes to aerial respiration is the fact that the great majority of fishes so adapted live in shallow tropical fresh waters. That this is so appears from the data given in the list on pages 354-5. A few of these fish, such as *Amia* and *Lepidosteus*, live outside the tropics, and in

* We owe this suggestion to Prof. J. Graham Kerr, F.R.S.

large rivers and lakes rather than in swamps. Two (*Misgurnus fossilis* and *Umbra krameri*) are found in muddy rivers and ponds in Europe. A few others are found in similar rivers in the tropics, and one (*Periophthalmus kolreuteri*) lives on muddy tropical shores and in mangrove swamps. These are the exceptions to the rule. It will be found that three-fourths of the fishes of the list live in shallow and stagnant fresh waters in the tropics. None are typically fishes of the larger tropical lakes, and none are truly marine.

It is to be expected that the breathing of air should have been evolved in waters in which there is a lack of oxygen. Thus the distribution of these fishes confirms the conclusion of the previous paper that such a lack of oxygen is a common characteristic of these waters. Similarly, the large proportion of air-breathing fishes among the fauna of the swamps of the Chaco supports the conclusions of the previous paper for this particular case. Reasons were also given in that paper for thinking that similar conditions occur in other types of tropical fresh water, especially in the slower and shallower parts of many tropical rivers. The fact that some of these fishes inhabit rivers of this type is therefore in favour of the conclusions of that paper rather than against them. A shortage of oxygen is undoubtedly a characteristic of foul waters everywhere. It is probable that aerial respiration in *Misgurnus* and *Umbra* is to be accounted for on these grounds.

In contrast to the conditions in the swamps and slow rivers, those in the rapid mountain streams, which have been investigated by Hora (1922-3), may be cited. These waters are undoubtedly more than usually rich in oxygen, and it is interesting to find that he describes adaptations which result in a reduction of the efficiency of the respiratory organs by a reduction in the respiratory current in many of the fishes of these streams.

The truth of these conclusions implies that aerial respiration in the fishes has been primarily an adaptation to life in a medium poor in oxygen, and not, as is often believed, to migration out of the water. It is undoubtedly true that many of these fishes use their power of breathing air to enable them to leave the water. Some habitually do so (*Anabas*, *Periophthalmus*), and others are able to avoid the dangers of a drought in this way (*Lepidosiren*, *Symbranchus*, *Callichthys*, etc.). It seems that this is a secondary use of the adaptations. The majority of these fish never leave the water. To them the adaptations are only of use in the water. Further, the shortage of oxygen is a danger which is continually present. To leave the water is not essential to the life of any fish, and a drought is an occasional phenomenon.

We see a possible starting-point for one type of these adaptations in the habit of some Cyprinidae (roach and bream, Evans & Damant, 1928) of regulating the hydrostatic pressure in their air bladders by inhaling or exhaling gas. Respiration must be carried on wherever an epithelium is in contact with air, and it is only necessary for the epithelium of the bladder to become more and more adapted for respiration, and for the exchange of gases to become more

and more regular, for this habit to result in the development of an accessory respiratory organ. It may be that this has been the course of the acquisition (*i. e.*, secondary re-acquisition) of the respiratory function of the air-bladder in the Teleosts, or it may be that its use as such is a persistence of the previous respiratory function of the bladder. If the latter is true, the lack of oxygen in tropical waters seems to have been of importance in preserving the respiratory function after it has been lost by other fish.

Whatever views are held on this subject, it seems that this lack of oxygen in tropical waters has played a large part in the evolution of the terrestrial vertebrates. It is generally held that the escape of the vertebrates from the water took place in some such environment. A power of breathing air must have been a necessary preliminary to the possibility of the migration. It appears probable that the development or the preservation of aerial respiration in this fish, as in other fishes of the tropical fresh waters, was a response to the shortage of oxygen in the water, and that it occurred while the fish was still purely aquatic. The fish was then ready for the later changes which completed the migration. The stimulus for these was probably provided by the droughts to which any animal living in such waters must have been subjected. That this has been the course of the later stages of the migration on to the land is generally accepted, but it does not seem to have been so generally realised that the first stage in the process of migration was the evolution of adaptations to aerial respiration, first instigated by the lack of oxygen in the shallow tropical fresh waters in which the fish lived.

SUMMARY.

1. In a previous paper the swamps of the Paraguayan Chaco have been shown to be an environment in which the fauna is exposed to great lack of dissolved oxygen. The adaptations by which the rich fauna of fishes in these swamps maintains its life under these conditions are discussed in this paper.

2. There are two accessory sources from which these fishes can obtain oxygen. These are :—

- (a) The air above the water.
- (b) The thin, well oxygenated, surface layer of the water.

Eight of twenty species collected in these swamps are adapted to breathe air and the rest all make use of the second of these sources.

3. The eight air-breathing species belong to seven genera and have six independent types of aerial respiration. The adaptations of two of these (*Lepidosiren* and *Symbranchus*) are not further discussed. In the other genera the organs of aerial respiration are :—

<i>Erythrinus</i>	Air-bladder.
<i>Hypopomus</i>	Gill-lamellæ.
<i>Callichthys</i> and <i>Hoplosternum</i> ...	Intestine.
<i>Ancistrus</i>	Stomach.

The accounts given by previous authors of the first and third of these types of aerial respiration are made more complete. An account is given of the adaptations of *Hypopomus* and *Ancistrus*. In each genus the structure and histology of the organ is described, and experiments are recorded which show that respiration is carried on in it.

4. In a discussion of aerial respiration in the fishes, the following points are considered :—

(a) The organ of aerial respiration is mainly one of oxygen-absorption. This is due to the greater efficiency of aquatic respiration with regard to the excretion of carbon dioxide in the gills, which are retained in these fishes.

(b) Only in *Hypopomus*, and probably in *Symbranchus*, are the gills adapted as organs of aerial respiration. This is perhaps due to the advantage to the fish of retaining the gills for the excretion of carbon dioxide.

(c) Except in those fishes which have a separate pulmonary vein to the heart, the blood is mixed throughout the circulation.

(d) The blood from the accessory respiratory organs hardly ever passes through capillaries on the way to the heart.

(e) The majority of these fishes live in shallow tropical fresh waters. Reasons are given for thinking that these adaptations are primarily for the maintenance of life in waters in which there is a lack of oxygen, and not for migration on to the land. Thus the suggestion made in the previous paper, that in general the fauna of shallow tropical fresh waters is exposed to a lack of oxygen, is confirmed.

5. These facts suggest that a preliminary step in the migration of fishes on to the land in the evolution of the terrestrial vertebrates was the development of aerial respiration in some such habitat as the tropical swamp, while the fish was purely aquatic, and in response to the conditions of this environment. The later migration was made more easy by this development. A further step in the series of changes leading to the migration was probably the habit of passing periods of drought in some semi-aquatic habitat, a habit which *Lepidosiren* and *Symbranchus* possess to-day.

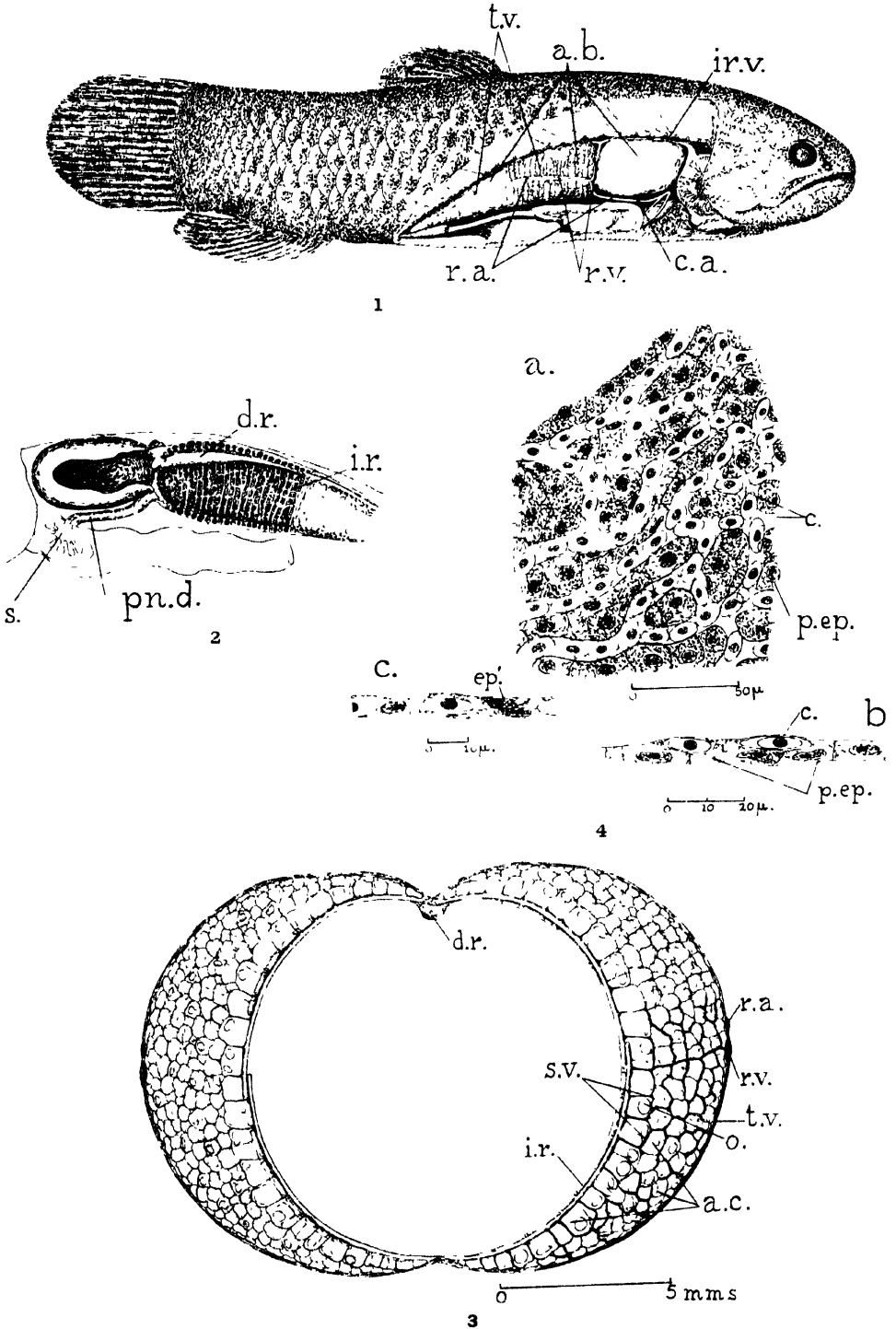
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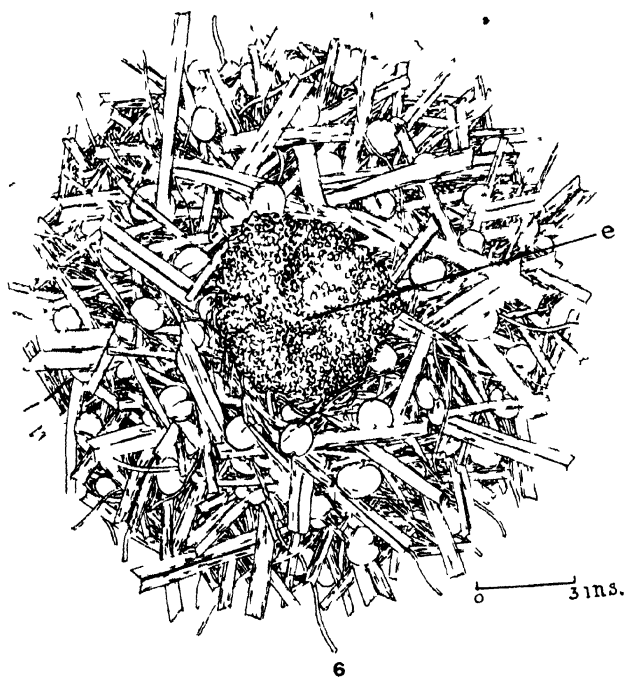
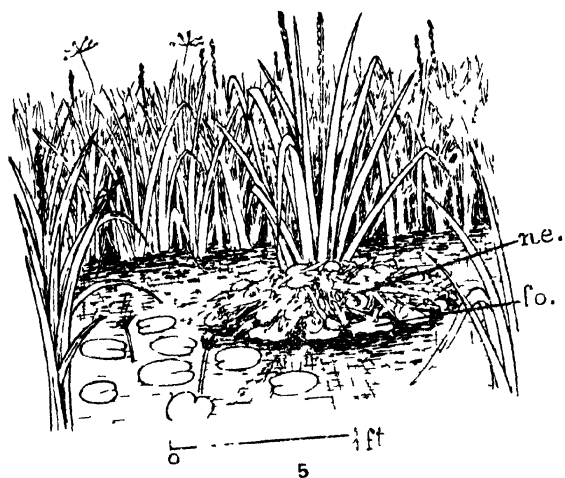
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EXPLANATION OF THE PLATES.

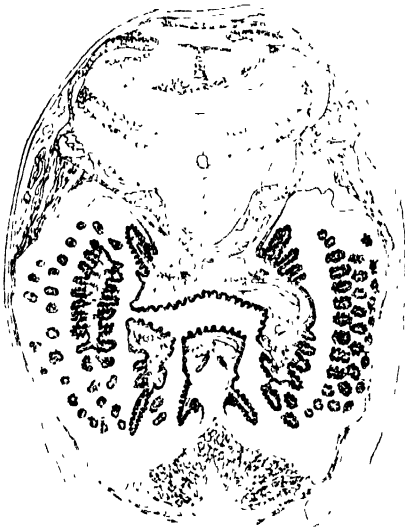
<i>a.</i>	atrium.	<i>g.</i>	gland.
<i>a.b.</i>	air-bladder.	<i>gf.</i>	gill-lamellæ.
<i>a.c.</i>	cells of the wall of the respiratory air-bladder of <i>Erythrurus</i> .	<i>h.</i>	heart.
<i>an.</i>	anus.	<i>i.</i>	intestine.
<i>a.s.</i>	artery to the stomach sac.	<i>i.ep.</i>	intestinal epithelium.
<i>c.</i>	capillaries.	<i>i.r.</i>	internal ridges of air-bladder.
<i>c.a.</i>	cœliac artery.	<i>ir.v.</i>	interrenal vein.
<i>c.ep.</i>	cœlomic epithelium.	<i>K., k.</i>	kidney.
<i>c.i.</i>	coils of the intestine.	<i>L.</i>	liver.
<i>d.a.</i>	dorsal aorta.	<i>m.</i>	muscle layers.
<i>d.r.</i>	dorsal ridge of air-bladder.	<i>ne.</i>	nest.
<i>e.</i>	mass of eggs.	<i>o.</i>	ovary.
<i>ep.</i>	epithelium.	<i>o.o.</i>	opening of oviduct.
<i>ep'</i>	point where the epithe- lium of the septum is two cells thick.	<i>œs.</i>	œsophagus.
<i>f.</i>	fat.	<i>op.</i>	openings between cells of the wall of the re- spiratory air-bladder.
<i>fo.</i>	foam.	<i>p.c.</i>	pillar cells.
		<i>p.ep.</i>	pavement epithelium
		<i>pn.d.</i>	pneumatic duct.



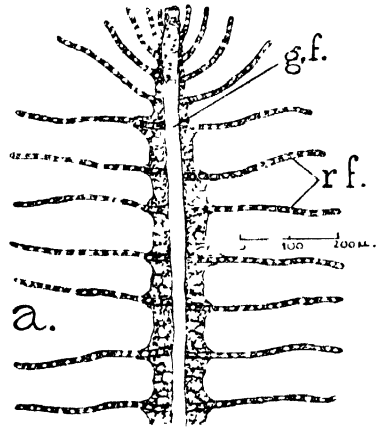
ERYTHRINIIS UNITÆNIATUS.



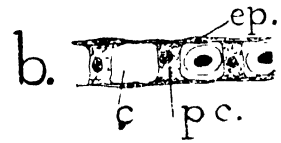
6
HOPLOSTERNUM LITORALE



7

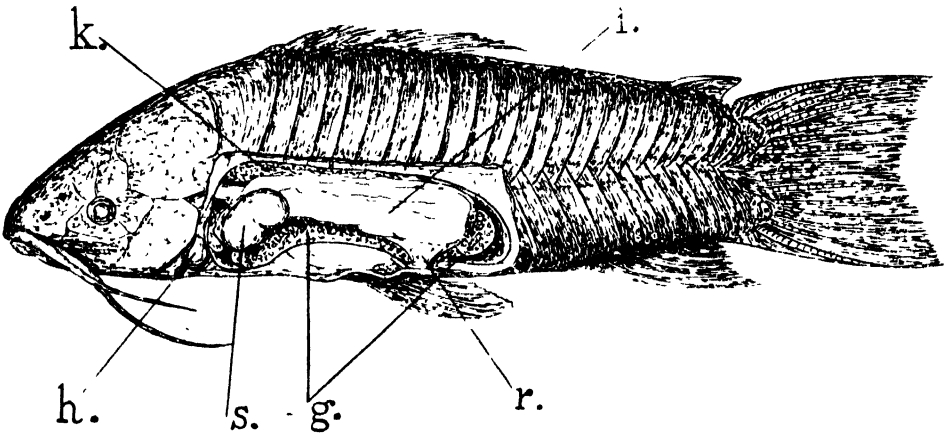


a.



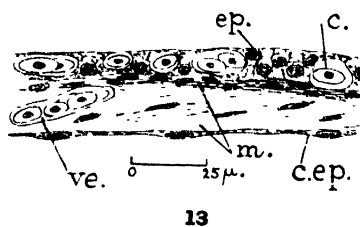
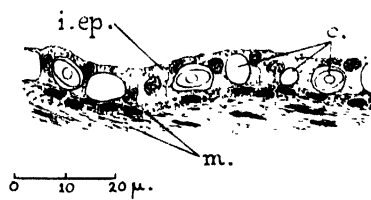
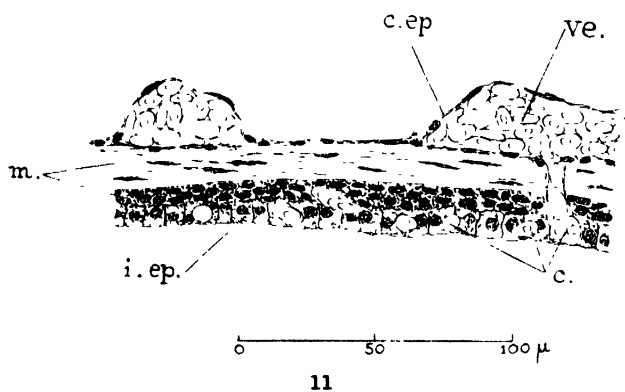
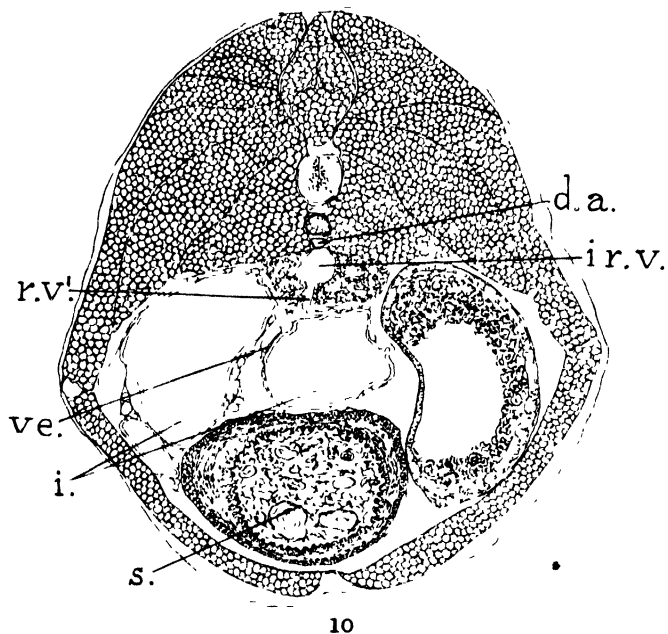
b.

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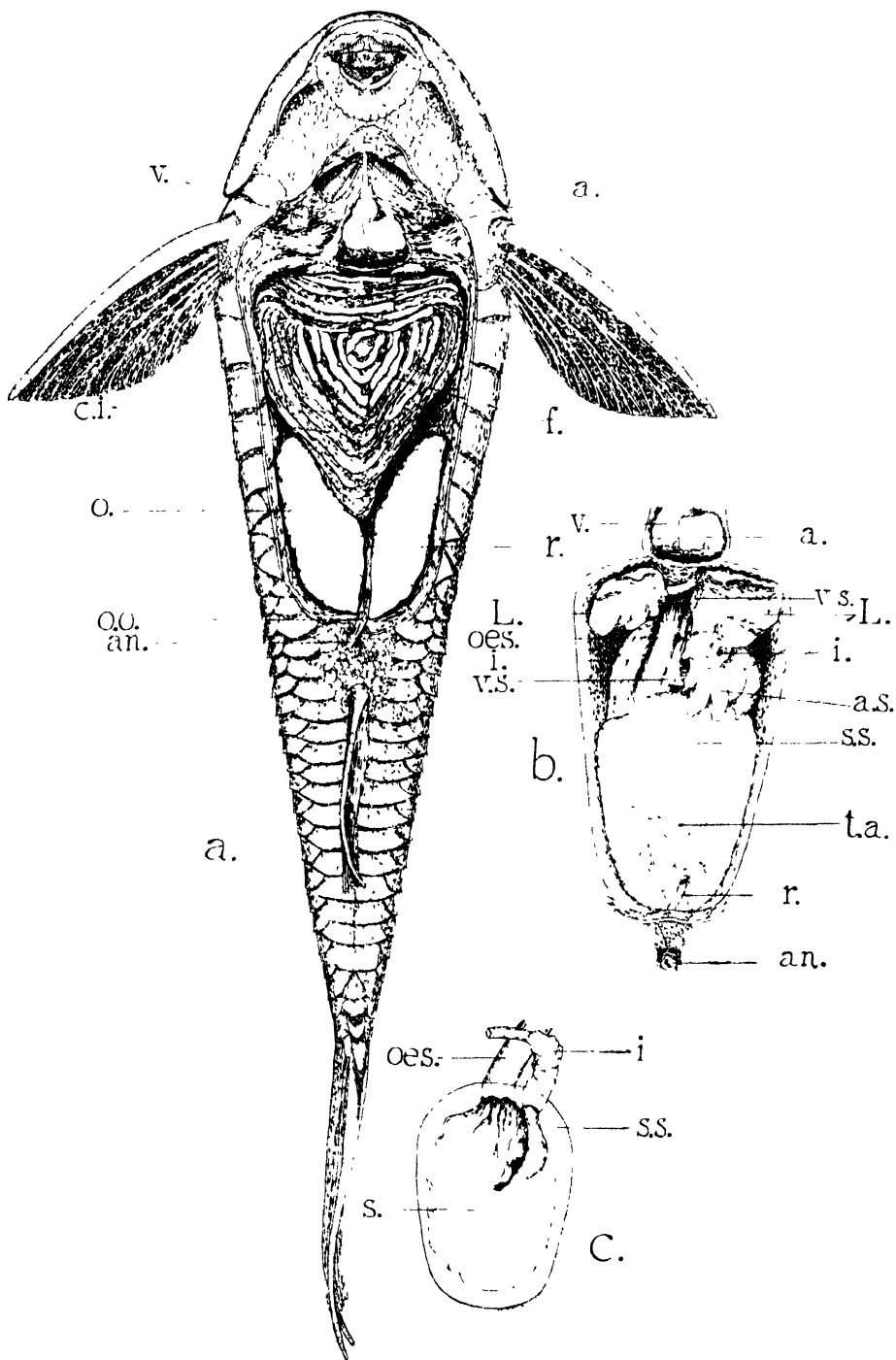


9

HYPOPOMUS BREVIROSTRIS. HOPLOSTERNUM LITORALE.



HOPLOSTERNUM LITORALE, ANCISTRUS ANISITSI.



<i>r.</i>	rectum.	<i>t.a.</i>	transparent area in wall of the sac.
<i>r.a.</i>	respiratory artery.	<i>v.</i>	ventricle.
<i>r.f.</i>	respiratory folds	<i>ve.</i>	small blood-vessel in wall of the stomach.
<i>r.v., r.v'.</i>	respiratory veins.	<i>v.s.</i>	vein to stomach sac.
<i>s.</i>	stomach.		
<i>s.s.</i>	sac which encloses the stomach.		

PLATE 19.

- Fig. 1. A dissection of *Erythrinus uniteniatus* from the right side. To show the structure of the air-bladder and the arrangement of the blood-vessels which supply it. $\times 3$.
- Fig. 2. The air-bladder of *E. uniteniatus* opened on the left side. To give a view of the internal surface of the wall and the arrangement of the pneumatic duct. $\times 1$.
- Fig. 3. A thick transverse section through the respiratory part of the wall of the air-bladder of *Erythrinus uniteniatus*. To show the arrangement of the layers of thin-walled cells in the thickness of the wall. The distribution of the veins in the septa between these cells is shown in the lower part of the figure on the right side. Their size is exaggerated in order to make their distribution clear.
- Fig. 4. The histology of these septa —
- (a) A surface view of a septum showing the capillary network.
 - (b) A transverse section of a septum.
 - (c) A similar section where the septum is two cells thick.

PLATE 20.

- Fig. 5. A drawing of the nest of *Hoplosternum litorale* on the surface of the swamp. The raft of dead sticks and leaves (*ne.*) is at the foot of the central clump of sedge. The foam which covers the underside of the nest can be seen at its edge (*fo.*).
- Fig. 6. The underside of the same nest after it has been removed from the water. To show the central mass of eggs.

PLATE 21.

- Fig. 7. *Hypopomus brevirostris*. Transverse section of the mouth and gill chamber.
8. *Hypopomus brevirostris*,
- (a) A longitudinal section through the gill-lamella and the secondary folds attached to it.
 - (b) An enlarged drawing of part of a similar section of a fold.
- Fig. 9. *Hoplosternum litorale* dissected to show the arrangement of the parts of the alimentary canal. The left gonad and parts of the kidney and liver have been removed. $\times 1$.

PLATE 22.

- Fig. 10. *Hoplosternum litorale*. A transverse section through the body of a larva 22 mm long, in the region of the kidney. To show the origin of the smaller respiratory veins from the interrenal vein through the kidney.

- Fig. 11. *Hoplosternum litorale* (adult). A section of the wall of the respiratory intestine. To show the arrangement of the muscle layers and the supply of the capillaries from veins on the outside of the wall.
- Fig. 12. *Hoplosternum litorale* (adult). The intestinal epithelium and the capillary network in section.
- Fig. 13. A transverse section through the respiratory wall of the stomach in *Ancistrus anisitsi*, from a larva 30 mm. in length.

PLATE 23. *

- Fig. 14. *Ancistrus anisitsi*. Three dissections of the contents of the body-cavity. In (a) only the ventral body-wall has been removed. In (b) the arrangement of the organs after the removal of the coiled intestine and the gonad is shown. In (c) a view of the inner side of the ventral wall of the stomach sac and of the stomach attached to it is given. All $\times \frac{3}{2}$.

On a new Species of the Genus *Hoplophorus* [*Oplophorus*] H. M.-Edw., *Hoplophorus novæ-zeelandiæ*, sp. n. By [the late] Dr. J. G. DE MAN, Ierseke, Holland. (Communicated by Dr. G. P. BIDDER.)

(With 20 Text-figures.)

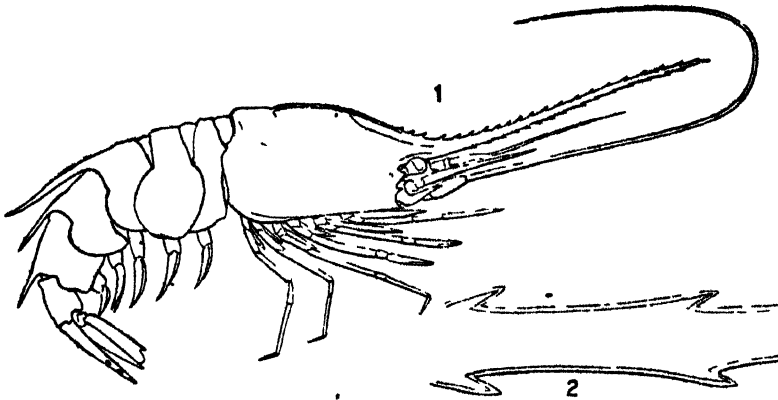
[Read 6th November, 1930.]

ON March 19th, 1929, I had the honour to receive a letter, dated February 9th, from Professor R. Speight, of the Canterbury Museum, Christchurch, New Zealand, in which he informed me that he would send me for identification a species of shrimp, specimens of which had been presented to that museum. These shrimps were taken from the stomach of a groper (*Polyprion prognathus*), captured in two fathoms of water off Kaikoura, on the east coast of the South Island of New Zealand, a well-known fishing ground with lines, where the deep water comes to within a short distance of the shore. Four full-grown specimens, one of which is provided with eggs, were received, but unfortunately all are more or less damaged and broken.

After a thorough examination they proved to belong to a new species of the genus *Hoplophorus* H. M.-Edw., distinguished probably from all the known species of this genus by the outer margin of the antennal scale being *smooth* and *unarmed*—I say probably, because this margin is perhaps also smooth in *H. spinicauda* A. M.-Edw., a species collected by the 'Travailleur,' July 1882, at a depth of 636 m., according to the figure in the 'Recueil de Figures de Crustacés nouveaux ou peu connus,' published by A. Milne-Edwards in 1883. *H. spinicauda*, however, of which unfortunately a description does not exist, differs at first sight from *H. novæ-zeelandiæ* by the termination of the 2nd segment of the abdomen in a spine.

In no one of the four specimens is the rostrum complete, so that the exact length could not be indicated with certainty. In one specimen the carapace, measured in the mid-line from the posterior border to the orbital margin, proves to be 17 mm. long, the still existing part of the rostrum 28 mm.; the rostrum of this species is therefore probably *twice* as long as the carapace. This specimen is broken and much damaged. In another, a male, which is the best preserved and therefore the specimen which will be described, the carapace is also 17 mm. long, the abdomen 44 mm., so that the whole length may be estimated at 95 mm. Of the ova-bearing specimen, of which the carapace is broken, the abdomen is 40 mm. long, so that the female appears but little shorter. In its outer appearance (fig. 1) this species much resembles *H. longirostris* Bate (Report 'Challenger,' Macrura, pl. cxxvii, fig. 2). The much compressed carapace, 17 mm. long

as already mentioned, shows its greatest height of 12·5 mm. a little before the posterior border, and, the height decreasing forward, is 8 mm. high at the level of the antero-lateral angle, from the posterior border to the hardly perceptible cervical groove, viz. nearly along its posterior third part, the upper border of the carapace is obtusely carinate, even a little flattened, and on either side of the carina the surfaces of the cardiac region appear somewhat uneven. From this point forwards the carina is sharp and continued into the upper border of the rostrum; from about the middle of the carapace the upper border slopes downward, turning obliquely upwards again at the level of the 2nd antennular segment. The rostrum is narrow, straight or slightly curved, its upper border, as far as one can judge, armed probably with 15 or 16 teeth (figs. 1 and 2) (in

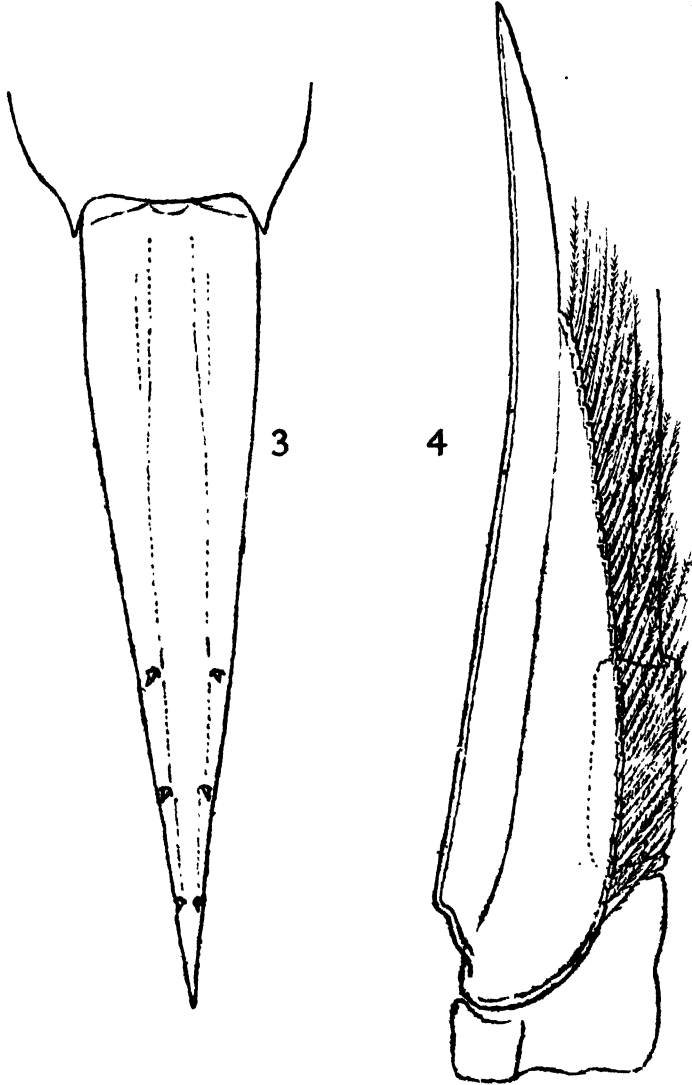


Hoplophorus novae-zeelandiae, sp. n.

1. Full-grown male, $\times 1\cdot2$. 2. Part of distal half of rostrum, $\times 12\cdot5$.

fig. 1 there are drawn perhaps 4 or 5 teeth too many); of these teeth the 2nd is placed above the orbital margin, the first 5 or 6 grow gradually a little longer, the following teeth become gradually smaller; the lower border bears a few less teeth, and on either border the distances between the teeth become anteriorly a little longer. From just before the eyes, at either side of the rostral carina, a sharp crest proceeds backward, parallel with the rostrum almost to the middle of the carapace, as in *H. typus* H. M.-Edw., of which the ova-bearing female from Stat. 46 a and the male from Stat. 17 'Siboga' Expedition are lying before me. As regards the sharp crest above the eye, the spines on the anterior border of the carapace, the longitudinal groove posterior to the antennal spine, the shape of the posterior border and of the lower border, this species agrees with *H. typus*, except that there is no tooth or spine on the postero-lateral angle of the carapace, as in *H. spinicauda* A. M.-Edw., *H. grimaldii* Cout., and *H. foliaceus* Rathb.

As in *H. typus* H. M.-Edw. and *H. grimaldii*, the 3rd, 4th, and 5th abdominal segments terminate in a spine; the spine of the 3rd, which is slightly curved upward, proves to extend to the posterior margin of the 5th segment; this seg-



Hoplophorus novae-zeelandiae, sp. n.

3. Telson, $\times 10$. 4. Scaphocerite, $\times 10$.

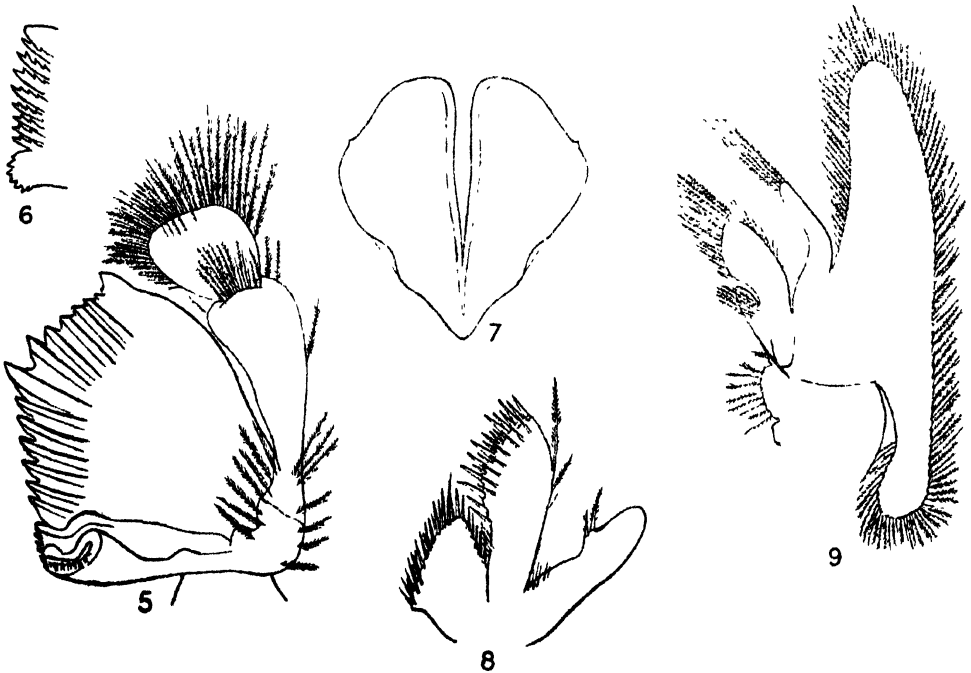
ment is pressed against it and is sharply carinate; the spines of the 4th and 5th are of equal length, rounded above and little more than half as long as the 3rd.

The 1st abdominal segment is carinate on its posterior half ; the 2nd, measured on its upper border, is twice as long and obtusely carinate, the tergum being slightly concave on either side of it ; the three following segments are nearly of equal length ; the 5th, one and a half times as long as the 2nd, is one and a half times as broad with the upper surfaces rounded. Telson (fig. 3) nearly *twice as long* as the 6th segment, *elongate-triangular, tapering*, 5 times as long as broad at base, probably terminating in an acute point ; its upper surface is flattened, faintly grooved anteriorly, and bears three pairs of small spinules on its posterior half, of which the anterior pair is situated just behind the middle and the middle pair nearly as far from the anterior as from the posterior. Uropods *a little shorter* than telson : inner uropod a little shorter than the outer.

In the full-grown male the anterior margin of the 1st pleuron runs from the triangular tooth or prominence at first straight downward, then curves to the lower border, which anteriorly is emarginate, concave, while the greater posterior part is truncate, straight ; in the egg-bearing female the anterior margin is regularly curved, convex, the lower straight ; the anterior margin of the 2nd pleura, which in the female are much broader than in the male, makes in the latter an obtuse angle with the truncate lower border, but in the female this angle is rounded ; the pleura of the 3rd and 4th segments are lunate, excavated on the anterior and convex on the posterior margin, so that they are produced to a point at the infero-anterior angle, this point sharper in the 3rd than in the 4th ; the 5th differs from these two segments in having a distinct, slightly concave lower border which makes an obtuse angle with the convex posterior margin, while the anterior angle is rounded ; the 6th segment, a little shorter than the 5th, is one and a half times as long as it is deep or high, its lower margin is straight.

The eye peduncles and the inner antennæ agree with those of *H. typus* ; the 2nd joint of the antennular peduncle is twice as broad as long. The basal spine of the outer antennæ, which is not visible when the animal is looked at from above, being directed inward and covered by the scaphocerite, reaches almost to the middle of the terminal joint of the antennal peduncle ; it is elongate-triangular and produced to an acute point. Not only the outer surface of the spine, but also that of the basal segment is distinctly concave. In *H. typus*, however, it is only the outer surface of the spine that is concave, not that of the article itself, and while in *H. novæ-zeelandiæ* the lateral margins of the spine are straight, the upper appears in *H. typus* concave, the lower convex and more prominent. The antennal peduncle reaches barely beyond that of the upper antennæ ; the terminal joint is stout, not quite twice as long as broad in the middle on the outer side ; the scaphocerite (fig. 4), 14.5 mm. long in the full-grown male, is but little shorter than the carapace and five times as long as broad ; it consists of the scale, the inner margin of which is fringed with hairs, and the acuminate spine, which measures almost one-third of the whole length and is distinctly separated from the scale on the inner margin ; the outer margin of the scaphocerite is *quite smooth, devoid of teeth or spines*.

The red-coloured incisor and molar processes of the unequal mandibles are distinct, but almost confluent, the molar process much smaller than the other : in one mandible the incisor process is armed between the molar process and the central tooth with 8 acute teeth that gradually grow larger toward the central tooth, and with 10 teeth beyond it, of which the first, contiguous to the central tooth, is the smallest, the second the largest, the six others gradually decreasing in size ; in the other mandible (fig. 5) there are only 6 teeth between the molar process and the central tooth and 8 beyond it ; the little tooth adjacent to the



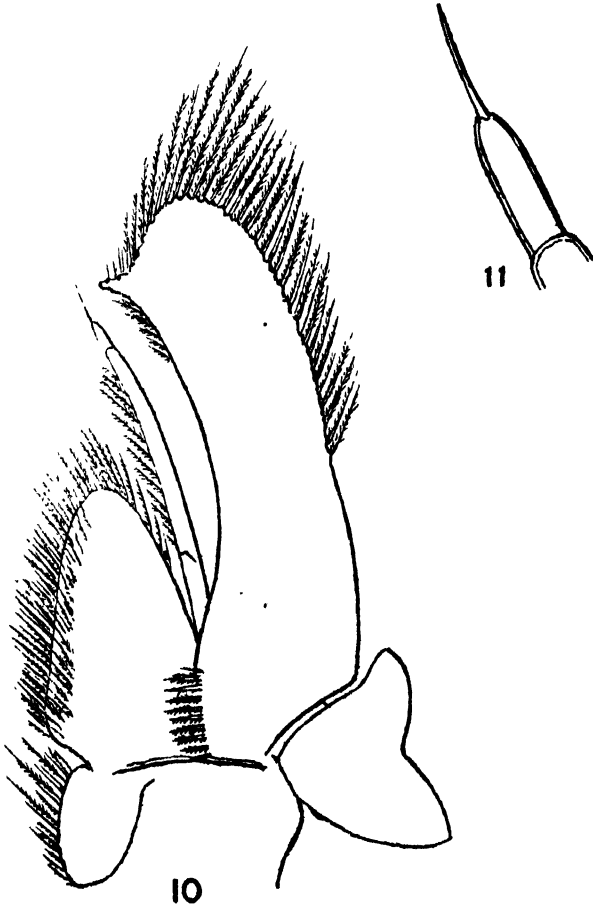
Hoplophorus novæ-zeelandiæ, sp. n.

5. Right mandible, looked at from the inner side, $\times 19$. 6. Spines on the molar process, $\times 50$. 7. Metastome, outer or posterior surface, $\times \frac{100}{9}$. 8. Right maxillula, looked at from the inner side, $\times \frac{100}{9}$. 9. Right maxilla, inner or anterior surface, $\times 100$.

central tooth is here wanting and the last tooth, with the very small penultimate on its inner border, appears almost as large as the first ; the free borders of the molar process are armed with uncoloured spines that present 2-4 small denticulations on their margin (fig. 6) ; palp 3-jointed, the terminal joint shorter, but broader than the preceding, and fringed with feathered setæ.

The two paragnaths that together form the metastome (fig. 7) are equal, gradually widening forward, with their antero-internal angle broadly rounded,

the anterior border S-shaped, with the antero-external angle somewhat angular. Of the two endites of the maxillulæ (fig. 8) the inner is broad, nearly as broad as long, with the outer border covered with spiniform and other setæ that are all feathered, and with microscopical spinules on the outer surface; the other endite is claviform, the smooth convex outer margin bears three setæ of un-



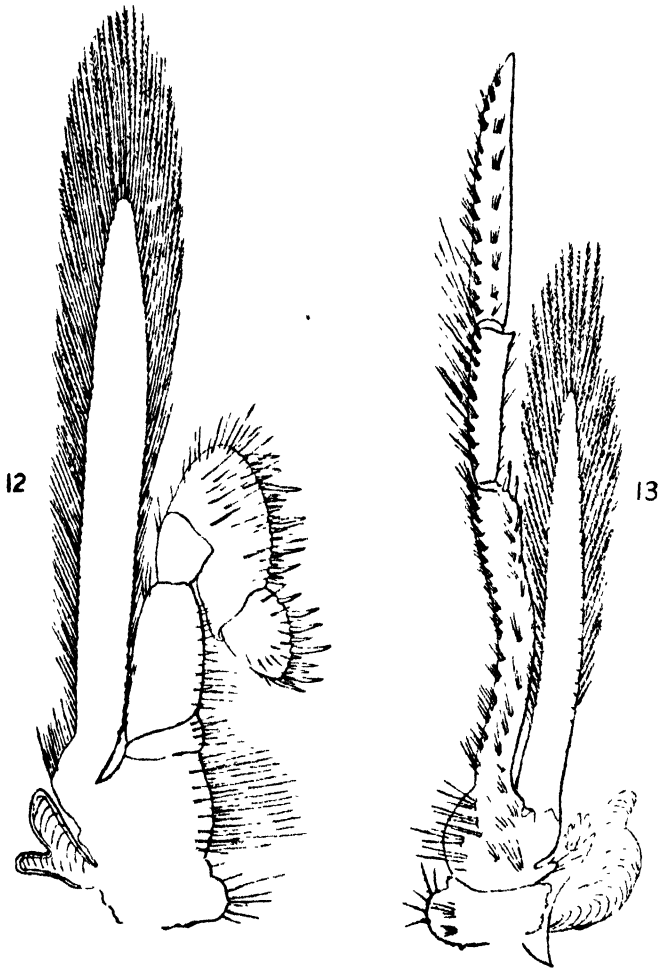
Hoplophorus novæ-zeelandiæ, sp. n.

10. Right maxilliped of 1st pair, $\times \frac{50}{3}$. 11. Terminal joints of the endopodite of this maxilliped, $\times 75$.

equal length, the distal half of the inner margin is armed with about a dozen strong acute spines and with nearly as many smaller ones, while the proximal half is fringed with feathered setæ; the palp, little shorter than the outer endite and the tip of which is obtuse, is glabrous, except for two setæ inserted on a triangular prominence a little beyond the middle; the longer, anterior seta

reaches to the tip of the palp, the other is only half as long: a third spiniform short seta occurs near that prominence on the outer surface.

The anterior endite of the maxilla (fig 9) is divided by a narrow incision into a rounded larger anterior and a smaller posterior part, the posterior endite by

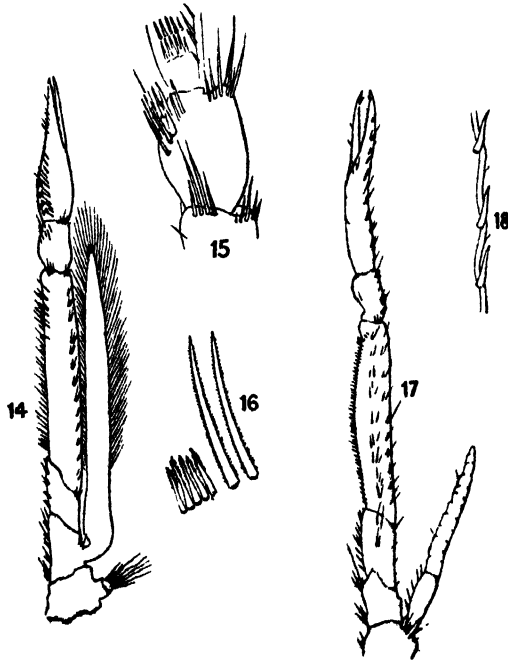


Hoplophorus novæ-zeelandiæ, sp. n.

12. Right maxilliped of 2nd pair, outer side, $\times \frac{100}{9}$. 13. Left maxilliped of 3rd pair, outer side. $\times 6.4$.

a short triangular notch into a very small anterior and a much larger posterior part; palp almost rectangularly bent, glabrous, except for a tuft of long feathered setæ on the rounded tip of the cylindrical distal part; scaphognathite with both extremities rounded, the posterior part shorter than the anterior.

The 1st maxillipeds (fig. 10) much resemble those of *H. typus* (H. Balss, 'Macrura der Deutschen Tiefsee Expedition,' 2. Natantia, Teil A, Jena, 1925, p. 248, fig. 22), but the prominence at the antero-internal angle of the falciform exopodite is very short, rudimentary, not segmented; basipodite twice as long as the coxopodite, terminal joint (fig. 11) of the endopodite three times as long as broad at its base; epipodite well developed. The 2nd maxillipeds (fig. 12) resemble also those of *H. typus* (H. Balss, *l. c.* fig. 23), but the dactylus that articulates with the distal end of the propodus is but *little longer than broad*,



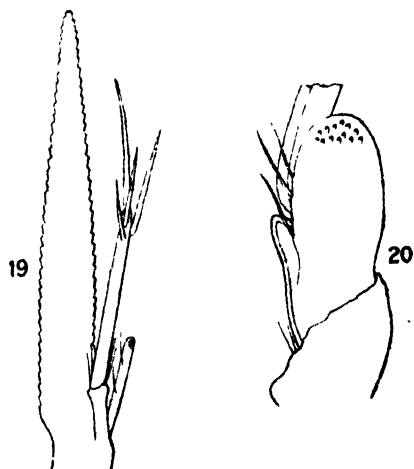
Hoplophorus novae-zeelandiae, sp. n.

14. Leg of 1st pair, $\times 5$. 15. Carpus of this leg, $\times 12.5$. 16. Spiniform bristles on the proximal part of the carpus, $\times 50$. 17. Leg of 2nd pair, $\times 5$. 18. Spines on the cutting edge of the dactylus, $\times 50$.

and thus broader than in that species; its inner (morphologically outer) margin is armed with 8 larger and 5 or 6 smaller spines, while on the outer surface setæ are implanted; the inner margin of the propodus bears 5 larger and about a dozen smaller spines; the outer surface is also setose; epipodite well developed. The external maxillipeds (fig. 13) are slender, and project with half the terminal joint beyond the antennal peduncle; the tapering terminal joint, 5.1 mm. long and ten times as long as broad at its base, is thickly covered with pectinated stiff bristles that are arranged in transverse rows;

the penultimate joint is 2.7 mm. long, five times as long as broad in the middle and little more than half as long as the terminal, its outer surface covered on the inner half with long setæ; the antero-external angle of the antepenultimate joint bears two spines behind one another, the anterior 0.5 mm. long, the posterior 0.4 mm. The foliaceous exopodite extends almost to the middle of the penultimate joint of the endopodite.

The legs of the 1st pair (fig. 14) reach almost to the distal extremities of the antennal peduncle; those of the 2nd are but little shorter, those of the 3rd extend to the same distance, the 4th reach to the distal margin of the 2nd antennal segment, the 5th a little shorter than the 4th. The palm of the 1st legs is a little more than half as broad as long and about $\frac{1}{8}$ shorter than the fingers: the lower



Hoplophorus novæ-zeelandiæ, sp. n.

19. Endopodite with stylamblys and appendix masculina of the 2nd pleopod of the full-grown male, $\times 10$. 20. Outer view of the stylamblys of this pleopod, $\times 20$.

border of the chela is ridged, and another ridge runs on the inner surface of the palm obliquely from the carpal articulation on to the immobile finger; these ridges are fringed at the inner side with setæ, while the rest of the palm is smooth and glabrous. The carpus bears a short tooth on the distal border at the lower side; exopodite foliaceous, reaching to the middle of the carpus. The chela of the 2nd leg (fig. 17) is one-third that of the 1st: the finger is nearly as long as the palm, which has a much slenderer form than that of the 1st, being 3.6 times as long as broad: the prehensile edges are armed, like those of the 1st legs, with numerous movable spines that are 0.1 mm. long, 12 to 14 on each finger (fig. 18): the carpus appears also longer in proportion to its breadth than in the 1st legs, and the merus is armed at a short distance from its

distal extremity with a stout spine 0.3 mm. long. Exopodite not foliaceous, reaching to the middle of the merus.

Dactylus of 3rd and 4th legs styliform, *half as long* as their propodi, terminating in a slender, tapering, slightly curved claw, measuring one-fifth the whole length of the dactylus; propodi eight or nine times as long as broad in the middle, slightly narrowing distally.

Propodus of 5th legs fifteen times as long as broad; dactylus about one-ninth of propodus, sugar-loaf-shaped, not quite twice as long as broad, clothed on the distal half with many long setæ of different length, some of which are pectinated, others feathered.

Endopodite and exopodite of the pleopods rather narrow; of the pleopods of the 2nd pair of the male the stylamblys is 1.2 mm. long, *foliaceous* (figs. 19 and 20), *lamelliform, rounded, twice as long as broad*, one margin—not the other—bearing three long setæ, the outer surface near the tip provided with a cluster of small cincinnuli. Appendix masculina (fig. 19) styliform, implanted a little in front of the stylamblys (figs. 19, 20) on a claviform part of the endopodite and 2.25 mm. long, almost twice as long as the stylamblys, and provided on and near the distal extremity with 4 or 5 long, spiniform setæ, of which the longest measures 1.65 mm., three-fourths the length of the appendix; these setæ are pubescent, covered with microscopical hairs.

The key for determining the species of the genus *Hoplophorus* which was proposed by Prof. Balss (*l. c.* p. 247) should now be changed as follows:—

- | | | |
|--------------|--|---|
| α . | Second segment of abdomen armed with a spine | } <i>spinicauda</i> A. M.-Edw.
<i>foliaceus</i> Rathb. |
| α_2 . | Second segment of abdomen unarmed. | |
| b_1 . | Outer margin of scaphocerite serrate. | |
| c_1 . | Scaphocerite tapering, both margins converging to the acuminate, spiniform, distal extremity; postero-lateral angle of carapace armed with a spine | <i>typus</i> H. M.-Edw. |
| c_2 . | Scaphocerite hooked distally. Postero-lateral angle of carapace unarmed | <i>grimaldii</i> Cout. |
| b_2 . | Outer margin of scaphocerite smooth. Postero-lateral angle of carapace unarmed | <i>novæ-zeelandiæ</i> de Man. |

Reports of an Expedition to Brazil and Paraguay in 1926-27, supported by the Trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for Scotland.

The Fauna of the Swamps of the Paraguayan Chaco in relation to its Environment.—III. Respiratory Adaptations in the Oligochæta. By G. S. CARTER, M.A., Ph.D., F.L.S., Lecturer in Zoology in the University of Glasgow, and L. C. BEADLE, B.A., Pembroke College, Cambridge.

(With 4 Text-figures.)

[Read 16th April, 1931.]

THE Oligochæta collected by the present authors in the Paraguayan Chaco have been systematically described elsewhere (Stephenson, 5). Those of the species which live in the swamps of the Chaco are exposed to an environment in which a continual lack of dissolved oxygen is the most unfavourable condition (1). The adaptations by means of which they are able to withstand these conditions are the subject of this paper.

Everywhere in the Paraguayan Chaco the rarity of the oligochætes is striking. This is equally true of the earthworms, which are usually only to be found where the ground has been recently cultivated, and of the aquatic Oligochætes, both in the swamps and in the other fresh waters, such as rain-water pools in the pastures and the saline pools which at most times of the year occupy the gulleys of the numerous streams.

In the swamps eight species of Oligochæta, including two of *Æolosoma*, were collected.

The species of *Æolosoma* were found among the weeds which cover the surface of many parts of the swamp. They thus belong to the surface fauna of the swamp, which is not subjected to so marked a lack of oxygen as that of the lower layers of the water. In this position they should find no more difficulty in satisfying their need for oxygen than the planktonic Crustacea and Rotifera, which are also to be found here, and the numerous species of fish, which obtain their oxygen from the surface layer of the water (2).

Four of the remaining six species (*Aulophorus borellii*, *A. beadlei*, *A. pectinatus*, and *Pristina macrochæta*) are to be found in the soft mud which forms the bottom of the swamp. The lower layers of the water above the mud have been shown (1) to contain no measurable amount of oxygen for long periods, especially during the hotter months of the year. The means by which the worms survive at these times could not be accurately determined. They were never abundant, and became fewer as the season became hotter. Some specimens of *Aulophorus borellii*,

kept in closed bottles of swamp-water, were found to live for 1-2 days after the water was completely deoxygenated, so far as the experimental method allowed it to be determined (less than .02 c.c. per litre), but none lived for a longer time in these conditions. In these experiments one or two worms, about 20 mm. long and less than $\frac{1}{2}$ mm. in diameter were enclosed in approximately 125 c.c. of water. It is therefore unlikely that the worms died from the accumulation of their excretions. It is probable that their minimum oxygen need is very low, but the experiments make it improbable that they are able to live anaerobically. Probably they are able to satisfy their small need for oxygen from the traces which occasionally reach the water in which they live, especially during the night and at dawn (1, p. 227). They were the only animals which were found in this position.

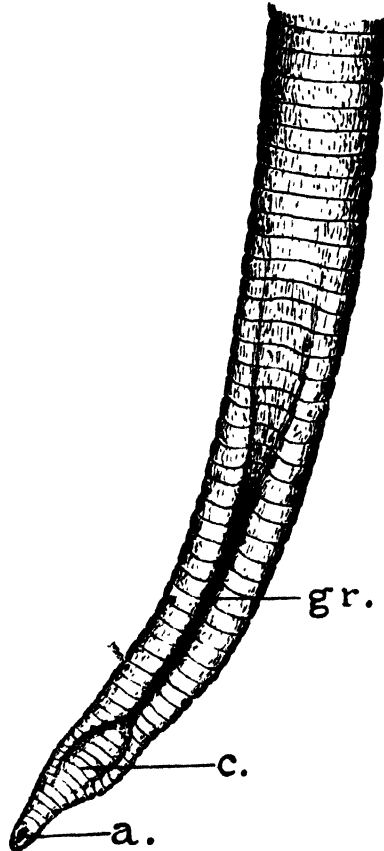
A fifth member of the Oligochaete fauna of the swamp (*Aulophorus carteri*) is, like the species of *Aelosoma*, an inhabitant of the surface-layers of the water. This worm has the habit of making for itself tubes (5-7 mm. long) of the spores and germinating prothalli of the water-ferns *Salvinia* and *Azolla*, which are abundant at the surface of the swamp. These materials are glued together by the worm by means of a secretion from the mouth. In this habit it resembles *A. tonkinensis*, an Asiatic species, described by Michaelsen (3) and Stephenson (4), which makes tubes of similar materials. In both species the tubes are cylindrical and open at both ends, from which the head or the tail of the worm may project. The worm crawls over the vegetation or floats at the surface of the water. The method of crawling is very like that of a leech, the head being extended and fixed by the mouth, which is used as a sucker. The tube is then drawn forward by contraction of the body.

The habit possessed by these worms of building a portable tube and so of leaving their natural habitat, the mud at the bottom of the swamp, and of living in the better oxygenated surface-layers must be regarded as an adaptation to life in an environment in which a lack of oxygen is the chief danger which the fauna has to meet. It is to be noted that both the species which have this habit are to be found in hot climates. It has been suggested (1, p. 251) that the shallow and stagnant fresh waters of the tropics are in general poorly oxygenated.

The only remaining Oligochaete found in these swamps is that with which this paper is chiefly concerned. This worm (*Drilocrius* sp.) is to be found in very shallow water (1"-3" deep) at the edge of the swamp. It was only found in the early months of the summer (Oct.-Dec.). It makes burrows in the mud and forms casts which may protrude above the surface of the water. It is a much larger worm than any of those previously described, being 70-100 mm. in length and 1-1.5 mm. in diameter. As in some other members of the same family (Glossoscolecidae) there is a groove (text-fig. 1, *gr.*) on the dorsal side of the body near the posterior end. This groove extends along the body for a variable distance (10-20 mm.). When it is contracted, it is deep (text-fig. 2),

but it can be almost completely opened out by the worm. Behind the groove, and opening into it, is a flattened cup-shaped area (c., text-fig. 1), which lies immediately in front of the anus. When the cast projects above the water, this cup-shaped area may often be seen to be protruded from the mouth of the burrow, forming an incomplete funnel opening into the groove and exposed to the air.

TEXT-FIG. 1.



Drilocrius sp. Dorsal view of the posterior part of the body.

- gr. groove.
 a. anus.
 c. cup-shaped area.

Some of these worms were kept in shallow dishes of water, in order that their habits might be observed. When the worms lay upon the bottom of the dish, and were covered with water so that no part of their bodies reached the surface,

they were occasionally observed to bend the posterior part of their bodies upwards, and to lay the groove, which was held open, in the surface-film. The groove was then closed over. Sometimes it could be seen that a bubble of air was enclosed within it. The posterior part of the body was then withdrawn from the surface, the enclosed air being carried down with it. The worms did not bend the posterior part of the body upwards in this manner, unless the water was shallow enough to allow it to reach the surface while the head of the worm remained on the bottom of the dish.

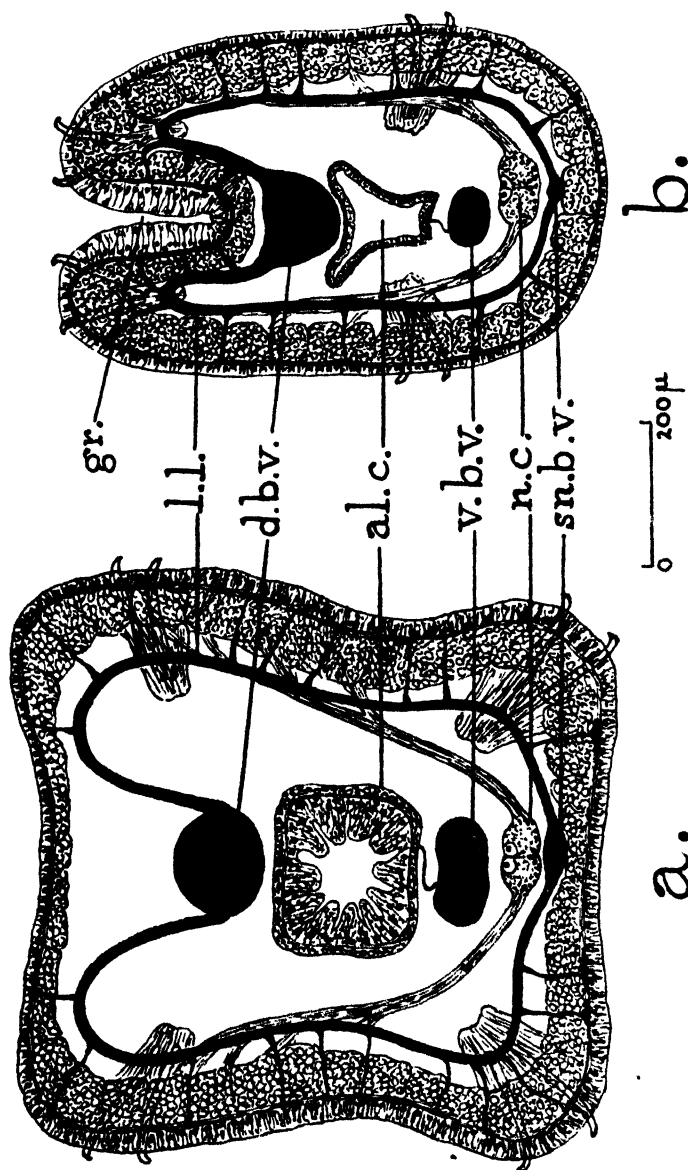
These observations suggest that the groove and the cup-shaped area behind it are parts of the body especially adapted for aerial respiration. The burrow is always filled with water, and, although the layer of water above the mud at the mouth of the burrow is often very shallow, it is probable that the water in the mud itself contains very little oxygen. This is certainly true of the mud in the deeper parts of the swamp, and the very active decay, which is shown to be going on wherever this mud is found by the large amount of gas present, indicates that it is in all probability true everywhere. If so, the worms will be forced to obtain their oxygen from the air or from the surface-film of the water. It would therefore not be surprising if some part of the body had become especially adapted as an organ of aerial respiration.

In order to test this possibility, the histological structure of the groove and the area behind it was examined. In text-fig. 2 drawings of transverse sections of the body in the region of the groove and in front of it are given, and in text-fig. 3 a drawing of a part of a similar section of the epithelium of the groove on a larger scale.

It will be seen that the epithelium of the groove is much higher than that of the rest of the surface, whereas in other parts of the body the epithelium on the dorsal side of the body is often lower than elsewhere. In text-fig. 3 it can be seen that the greater part of the thickness of the epithelium is due to the presence of very large numbers of well-developed gland-cells (*g.c.*), which lie everywhere between and below the much lower epithelium-cells (*ep.c.*). It is in the greater development of the gland-cells that this epithelium differs from that of the rest of the body. The dorsal blood-vessel is very large in all parts of the body, and the lateral loops are well developed. In the region of the groove these loops appear to be larger than elsewhere, especially where they lie below the epithelium of the groove, but their size varies greatly with the amount of blood in them, and it is difficult to be certain upon this point. The capillary branches, which are given off from these loops to the epithelium, are certainly much more numerous in the groove than on the dorsal side of other parts of the body. In the epithelium of the groove they can be traced without difficulty through the layers of muscle to the base of the gland-cells (*b.v.*; text-fig. 3).

In the hinder part of the groove there is a group of pits, usually arranged symmetrically on opposite sides of the median plane at the bottom of the groove.

TEXT-FIG. 2.



Drilocatus sp. Transverse section of the body. (a) in the centre of its length. (b) in the region of the groove.

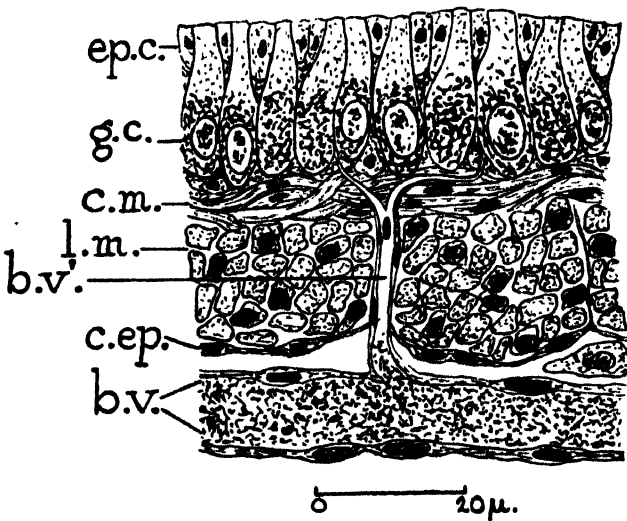
- | | | | |
|-----------------------|----------------------|------------------------|-------------------------|
| <i>a.l.c.</i> | alimentary canal. | <i>n.c.</i> | nerve-cord. |
| <i>d.b.v.</i> | dorsal blood-vessel. | <i>v.b.v.</i> | ventral blood-vessel. |
| <i>gr.</i> | groove. | <i>sn.b.v.</i> | subneural blood-vessel. |
| <i>l.l.</i> | lateral loops. | | |

In these pits the epithelium is much lower than that of the rest of the groove or on other parts of the body. We are unable to suggest any function which these pits may serve.

The epithelium of the cup-shaped area behind the groove is also higher than that of the rest of the body. It contains many gland-cells.

These parts of the body therefore show certain modifications which might be expected to occur in a region adapted for aerial respiration. The rich blood-supply is clearly such a modification, and it is probable that the increase in the size and number of the gland-cells is an adaptation towards the protection of the epithelium in its exposure to the air. In other animals, such as

TEXT-FIG. 3.



Drilocrius sp. Transverse section of the epithelium of the dorsal groove and of the underlying structures.

<i>b.v.</i>	blood-vessel.	<i>c.m.</i>	circular muscle.
<i>b.v'</i>	capillary blood-vessel to the epithelium.	<i>ep.c.</i>	epithelium-cells.
<i>c.ep.</i>	cœlomic epithelium.	<i>g.c.</i>	gland-cells.
		<i>l.m.</i>	longitudinal musculo.

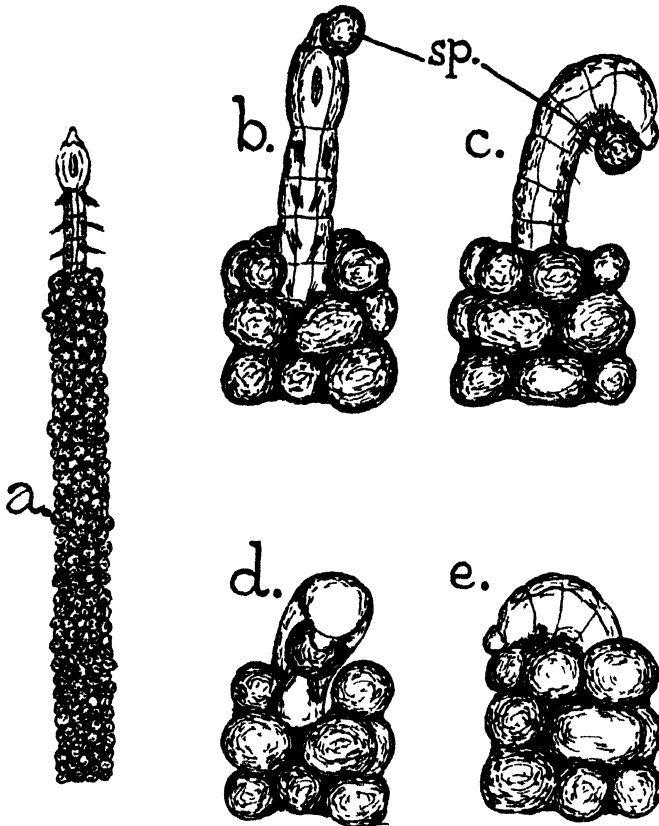
molluscs and land-planarians, the secretion of mucus over an unprotected epithelium is a well-known adaptation to an aerial habitat.

From this account of the adaptations of the *Oligochætes* found in these swamps, it will be seen that they show, either in their power of living in water with a low oxygen-content or in the means which they possess of obtaining oxygen in other ways, that a lack of sufficient oxygen for respiration is a danger to

which they are constantly exposed. These observations therefore support the conclusions of the previous papers

In conclusion, we should like to express our gratitude to Lt.-Col J. Stephenson, D.Sc., for much help in the course of this study.

TEXT-FIG. 4.



Aulophorus carteri.

a. The worm in its tube. From the ventral side. Length 5-7 mm.

b-e. Stages in the process of addition of a spore to the tube.

sp. spore.

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NOTE UPON THE METHOD OF TUBE-BUILDING IN *AULOPHORUS CARTERI*.
(Text-fig. 4, p. 385.)

The manner in which the tube of this species is built was observed by inducing some worms to make their tubes in open dishes. The worms were without tubes when they were taken from the swamp. They were placed in a dish of water provided with spores of the water-ferns *Azolla* and *Salvinia*, with germinating prothalli of these ferns and with seeds of larger plants. In nature, as a rule, only the spores of the water-ferns are used in making the tubes (text-fig. 4, *a*), which are thus very regular, except where some of the spores may have germinated and grown. In captivity it was found that the worms would make use of all the materials offered to them, and the tubes were therefore much less regular.

The method of building the tube is illustrated in text-fig. 4, *b-e*. The front end of the worm is protruded and a spore is caught by the prostomium (*b*). It is passed to the mouth (*c*), where it is rotated, probably by ciliary action, and presumably covered with an adhesive secretion. The front end of the body then bends upon itself (*d*), and the spore is placed in the centre of the bend. The mouth and prostomium, aided by the first few groups of setæ, place the spore in position on the wall of the tube (*e*), and it is held in this position for about 30 seconds. The hold may be temporarily relaxed, as if to test whether the spore is adhering securely. When the spore has been attached to the tube, the worm is ready to repeat the whole series of operations.

It seems of interest to find so complicated a chain of reflexes in a worm as simple as is this species. The process is also of interest in being very parallel to that of tube-building in many marine Polychætes (e. g., *Terebella litoralis*, A. T. Wilson, J. R. Microsc. Soc. 1890, p. 685).

An Account of the Development and Breeding-habits of a Brackish-water Polychæte Worm of the Genus *Marphysa*. By R. GOPALA AIYAR, M.A., Presidency College, Madras. (Communicated by Dr. E. S. RUSSELL.)

(With 31 Text-figures.)

[Read 20th November, 1930.]

THE mouth of the Adyar and the piece of backwater near the Madras Volunteer Guards Rifle Range, south of Mylapore (Madras), offers excellent collecting-grounds to the Marine Biologist. Here may be seen during the summer months from February to September, and in lesser numbers from December to February, numerous pear-shaped masses of jelly. These masses contain a large number of tiny black eggs scattered more or less evenly throughout their substance. When kept in a glass vessel with plenty of water the eggs hatch out readily. The larvæ were kept alive and the changes during their growth into adult worms were observed and noted down almost daily. Three or four sets of spawn-masses of the same age were kept developing at the same time and the various characters as they unfolded themselves were verified in each case. The following is the result of an investigation carried on for eight months and more. The great difficulty was to keep the larvæ alive by obtaining water almost daily from Adyar. Sea-water was tried, but the larvæ did not thrive in it. The diagrams given were made mostly from fresh material.

The Spawn-Masses.—These were found most abundantly during the summer months. The first heavy rain swells the amount of water in these backwaters and establishes a connection with the sea by opening up the usually closed mouth of the Adyar. This enables practically all the water in these places to empty itself into the sea. When this happens the spawn-masses are also carried out to the sea by the force of the outgoing current. During the rainy months the masses of spawn are but rarely seen. The masses are usually pear-shaped, but cylindrical masses are not rare. Whatever the shape, they are all provided with a long stalk which fixes them to the bottom, which in these places is of some consistency, formed mainly of clay with a small proportion of sand. I have never found them in purely sandy localities. A great number of them get torn from their stalks and may be seen floating on the surface of the water. When undisturbed and the wind light, as is very often the case in the mornings, they float vertically after the manner of miniature balloons, held in position by their stalks. Jelly-masses of recent formation are perfectly transparent, and the dark eggs may be seen shining through the thick gelatinous mass. But most of the masses that one sees in

these places are of a dirty colour, being invested by a covering consisting mainly of soft ooze and organic debris adhering to the outside of the jelly, forming an envelope which no doubt affords an additional protection. Multitudes of diatoms and other small organisms may be found gliding on the surface, but they do not seem to penetrate into the substance of the jelly. This may perhaps be due to a thin pellicle surrounding the jelly.

The Stalk of the spawn-mass is formed of a much denser material than the rest of it; it is continued some distance into the middle of the mass in the form of a dense core, round which the jelly is softer. The stalk is further strengthened by pellets of faecal matter passed out by the adult worm.

During the months of March, April, and May (as usual in summer) the water-level in the Adyar and the M.V.G. backwater goes down considerably. On the sides, the shore, in places for a yard or two, is covered with grass. On one occasion there was heavy rain some miles west of Madras; this water came down the Adyar and by the evening of the next day the grassy sides of the backwater were covered, but no spawn-masses were to be seen in the newly submerged places. The next morning when I paid my usual visit to the place I was surprised to find that an astonishingly large number of spawn-masses had appeared overnight in the newly submerged banks. The dust-bins, placed there by the military authorities to protect the sides of the sand-bank running across the backwater, which were perfectly dry with heaps of rubbish only, had also become partly submerged and inside them a few large spawn-masses had put in their appearance. The worms, which evidently had been living beneath the soil near the edge of the water waiting for a favourable opportunity, had all come up during the night and had discharged their ova along with the embedding jelly.

The same thing happened in another place also. Immediately south of the Cemetery on the road to Adyar there is a marshy level plain which was mostly dry. It is mainly covered during summer by *Seuda maritima*, and on the more southern side by small shrubs of *Avicennia* with a little forest of aerial roots round each. This marshy plain had also become submerged, and on the next morning numerous pear-shaped masses of spawn were found scattered throughout the plain and in among the roots of the *Avicennia*. Quite a different thing happened in the portion of the Adyar above the Elphinstone bridge. Here no spawn-masses had been formed. The water here had become greatly freshened on account of the influx of rain-water and not even the slightest trace of salinity could be detected, while the water in the M.V.G. backwater had not freshened to the same extent on account of its proximity to the sea. I have now observed the same thing occurring in other years also.

The above facts lead me to believe that the jelly-masses are formed at night, that very little time, probably only a few hours, is taken in their formation, and that the worms, though capable of living in soil submerged under water that is practically fresh, nevertheless discharge their ova only in water that is distinctly saline. There is no doubt that the form itself is capable of living

under water with a very low salinity for several months. It is suggested (1) that the jelly affords protection to the eggs from the sun's rays when the tide runs out and leaves them exposed; (2) that the jelly affords a safe place of development during the initial developmental stages; and (3) that it prevents wide dispersal of larvæ—an adaptation to backwater conditions.

Development.

Prototrochophore.—The eggs in the newly formed egg-masses are perfectly spherical with a transparent membrane. Fertilization probably takes place by the spermatozoa reaching the ova by penetrating the jelly. In 24 to 36 hours the spherical eggs which are $200\ \mu$ in diameter become uniformly ciliated, and the ciliated embryos begin to revolve slowly in the jelly (text-fig. 1).

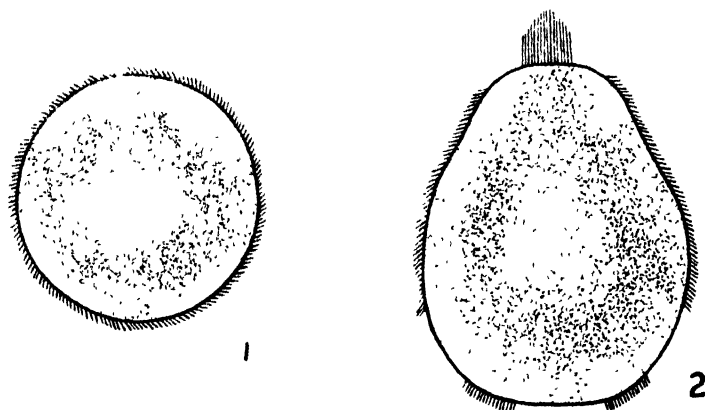


Fig. 1.—Uniformly ciliated stage. $\times 350$.

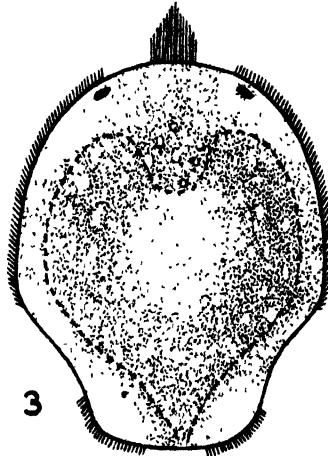
Fig. 2.—Very early metatrochophore. $\times 350$.

Twenty-four hours later, the spherical, uniformly ciliated embryos become slightly elongated, a little narrower in front than behind, with a uniform ciliation except at the front end where there is a tuft of fine cilia $3\frac{1}{2}$ to 4 times as long as the others. The ordinary cilia are $14\ \mu$ long, while the cilia of the apical tuft are $54\ \mu$ long (text-fig. 2). The body is mainly filled with greenish cells with a few round globules at the front end. The alimentary canal is not clear at this stage. The eyes have not become distinct. This stage evidently corresponds to the Prototrochophore stage of Hacker (6). There is no trochophore stage here, that stage being omitted from the life-history of the worm probably on account of the development taking place in the jelly.

Initial Metatrochophore.—But the above stage is very transient, and soon the uniform ciliation gives place to two bands of cilia. The first, a broad one, stretches from the level of the eyes to about three-fifths the length of the body from the anterior end. Behind the broad band there is a gap free from cilia and about one-fourth the total length of the body in extent. This is followed

by the second band of cilia, the extent of which varies slightly, but usually is half to two-thirds the breadth of the gap in front (text-fig. 3). This larva answers to the description given for the initial condition of the Metatrochophore stage of Hacker. The alimentary canal is distinct in this stage, is broad in front and narrowed behind. No lateral tufts of a longer set of cilia are discernible close to the posterior end of the front band of cilia. In this respect the larva of the present form differs from the Eunicid larva described by Gravely (10). In the gap between the two bands of cilia on each side, an invagination of the outer cuticle becomes observable. For a few hours this invagination appears, only to disappear again.

Late Metatrochophore.—A day later (*i. e.*, 24 hours after the restriction of the cilia to two ciliated bands) the invagination has become permanent,

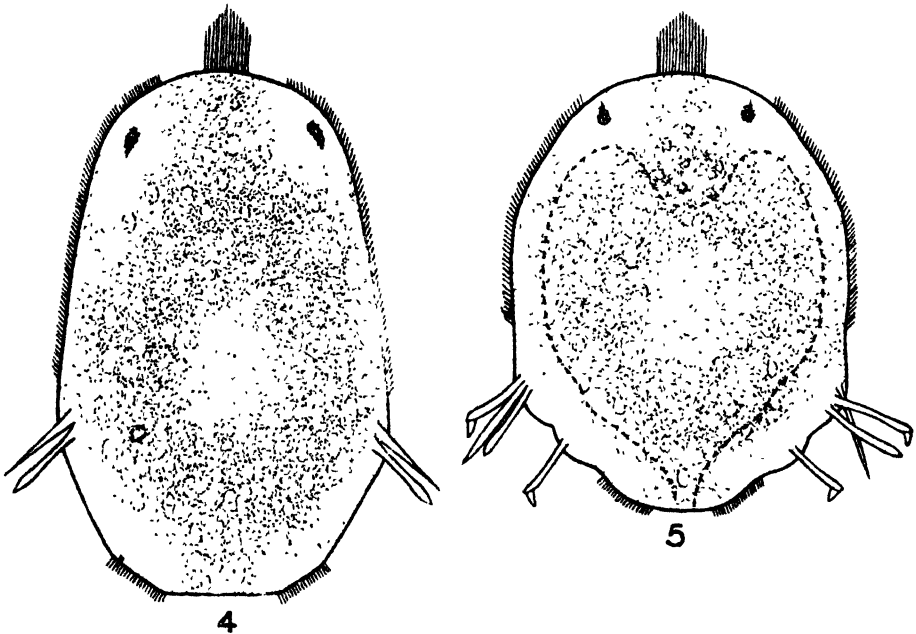


Initial metatrochophore with two bands of cilia, apical tuft,
and alimentary canal. $\times 350$.

and projecting from the base of it may be seen an unjointed pointed seta. This is soon followed by another, also unjointed, but differing slightly in shape from the first, being dilated at the end and drawn out into a short point (text-fig. 4). These two unjointed setae are always followed by a jointed seta of the hooked variety (text-fig. 5). These three setae on each side constitute the first pair of setose tufts. They are usually moved alternately, sometimes withdrawn completely into their pits, sometimes protruded. The larva moves with a screwing sort of rotatory motion, now and then seeming to contract and expand its body. It requires 48–60 hours for the spherical, uniformly ciliated embryos to become oval and acquire an apical tuft, two bands of cilia, and a pair of parapodia. Thirty-six hours later after the appearance of the first pair of parapodia the second pair of appendages appear in the form of a single jointed seta on each side (text-fig. 6). The cilia still continue to be the locomotor organs, the larva swimming slowly in the substance of the jelly. The

setose appendages are only rarely brought into play, as when the larva leaves the jelly and accidentally penetrates into the outer covering and so gets among a group of diatoms. The alimentary canal at this stage is sac-like, broad and clear in front, and abruptly narrowed behind (text-fig. 5). At the front end are a number of transparent globules of some nutrient substance. There is no trace of jaws at this stage. The larva measures $360\ \mu$ long, $230\ \mu$ broad, and obviously corresponds to the late Metatrochophore stage of Hacker.

One characteristic feature of this stage of development is that the first two pairs of setose appendages always appear in the unciliated gap between the two bands of cilia. In this respect the larva agrees with the Eunicid larva figured by Hacker (6) : it differs, however, from the Eunicid Metatrochophore



Figs. 4 & 5. - Late metatrochophores. $\times 350$.

larva figured by Gravelly in his "Polychæte Larvæ" (10, pl. i. fig. 21), where the setose tufts are shown as coming out of the region of the single broad ciliated band and each tuft is said to consist of three compound setæ. This is not the case in this form.

At this stage, of the three setæ of the first parapodia, the first formed is simple and pointed, the second blunt and dilated at the end, and the third is jointed. The larva at this stage does not exhibit that rotatory screwing movement which characterized its earlier stages, swims more evenly, rotates only occasionally, and uses its appendages more vigorously. The second pair of appendages soon come to consist of 3 setæ on each side, all of them compound and of the hooked variety (text-fig. 8).

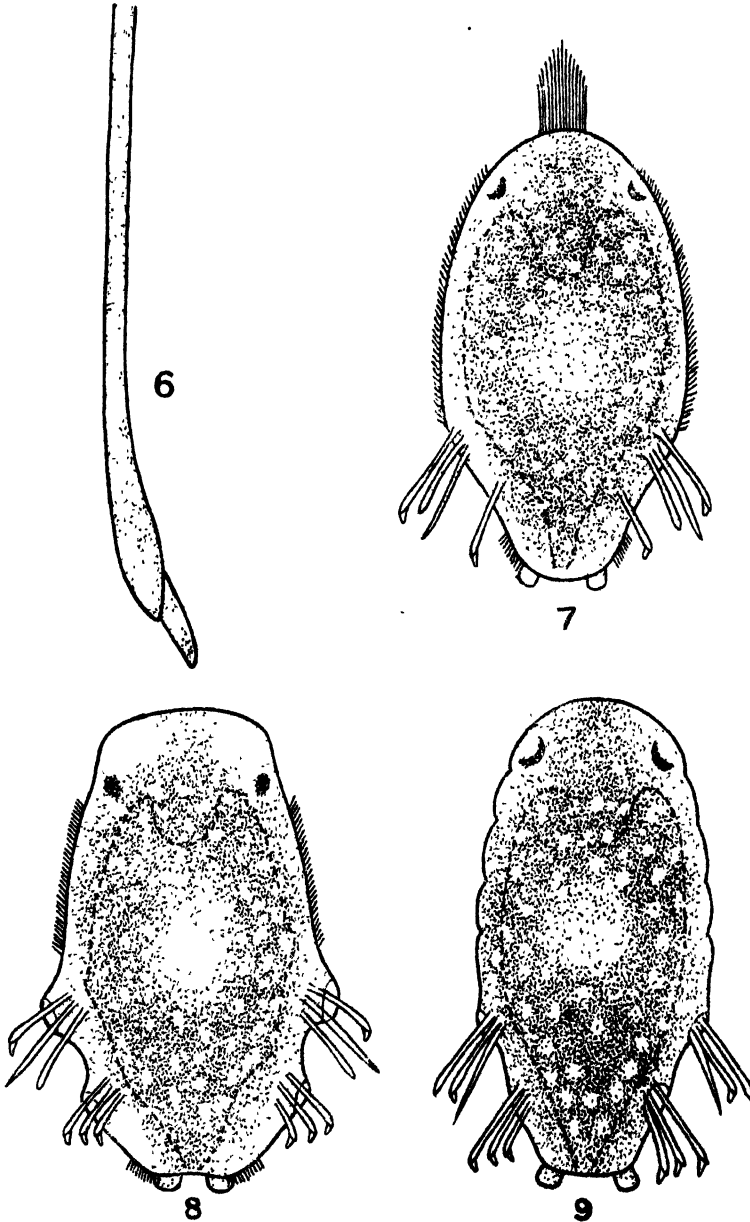


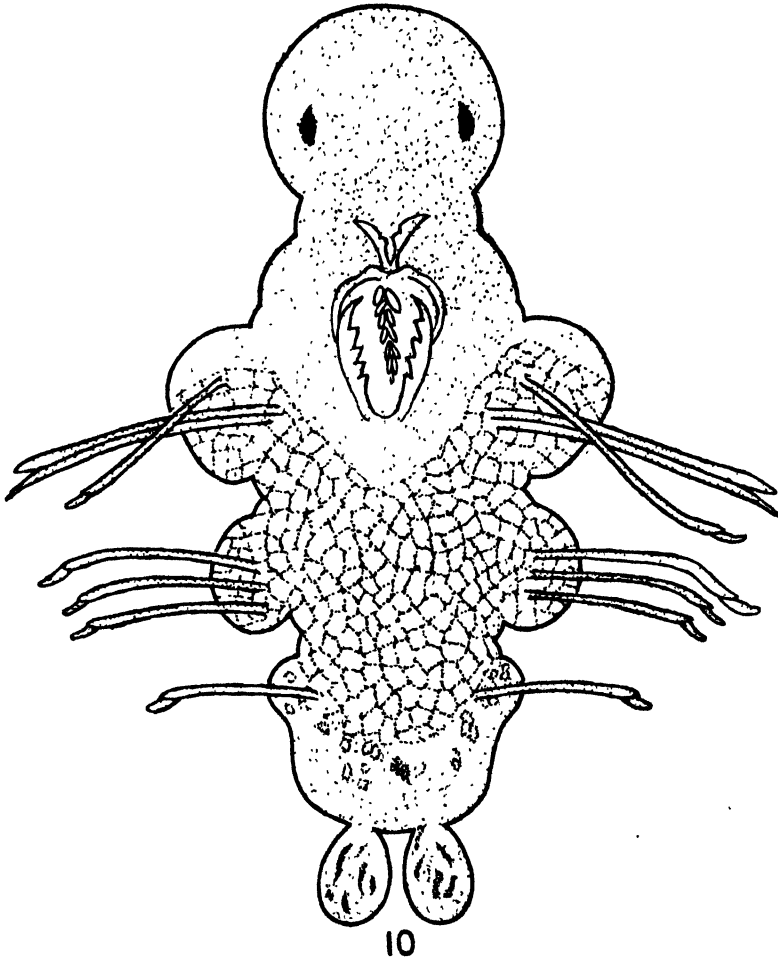
Fig. 6.—A single hooked compound seta. \times ca. 2000.

Fig. 7.—Late metatrochophore with three setæ in the first and one in the second tuft. A pair of anal styles present. \times 350.

Fig. 8.—Still later stage with two pairs of setose tufts, each with three setæ. Apical tuft gone. \times 350.

Fig. 9.—Corresponding to early Nectochæta, with anterior constrictions. Cilia absent. \times 350.

Nectochaeta.—Before the third pair of setose appendages are developed, a pair of almost globular, fleshy, transparent anal styles are formed at the posterior end (text-figs. 7 & 8). During this period the larva undergoes loss of cilia, the apical tuft disappearing first, rapidly followed by the broad and the narrow bands of cilia. When the cilia are completely gone the pear-shaped gelatinous mass gradually disintegrates, the non-ciliated larvæ sink to the bottom and commence their creeping mode of life.

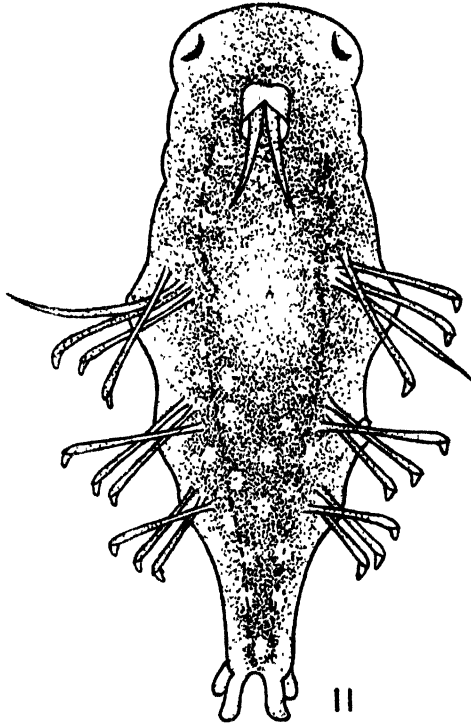


Corresponding to a young *Nectochaeta*. Specimen flattened out under pressure of coverslip. $\times 350$.

At the commencement of the creeping habit the body undergoes a slight elongation and becomes twice as long as broad (text-fig. 9). In front of the first parapodial segment paired constrictions appear indicating segmentation in this region. The larva then acquires a third pair of setose tufts, each at first

consisting of a single seta, but later on of three setæ all of which belong to the compound hooked variety (text-figs. 10 & 11). The first pair of chætigerous appendages meanwhile develop an additional compound seta on each side and each tuft therefore consists of four setæ, three of which may be jointed and one always unjointed. The succeeding two pairs of tufts are always provided with three compound setæ.

This stage in the development of the present form is markedly different from the corresponding stages of similar larvæ already described. Gravely (9) in



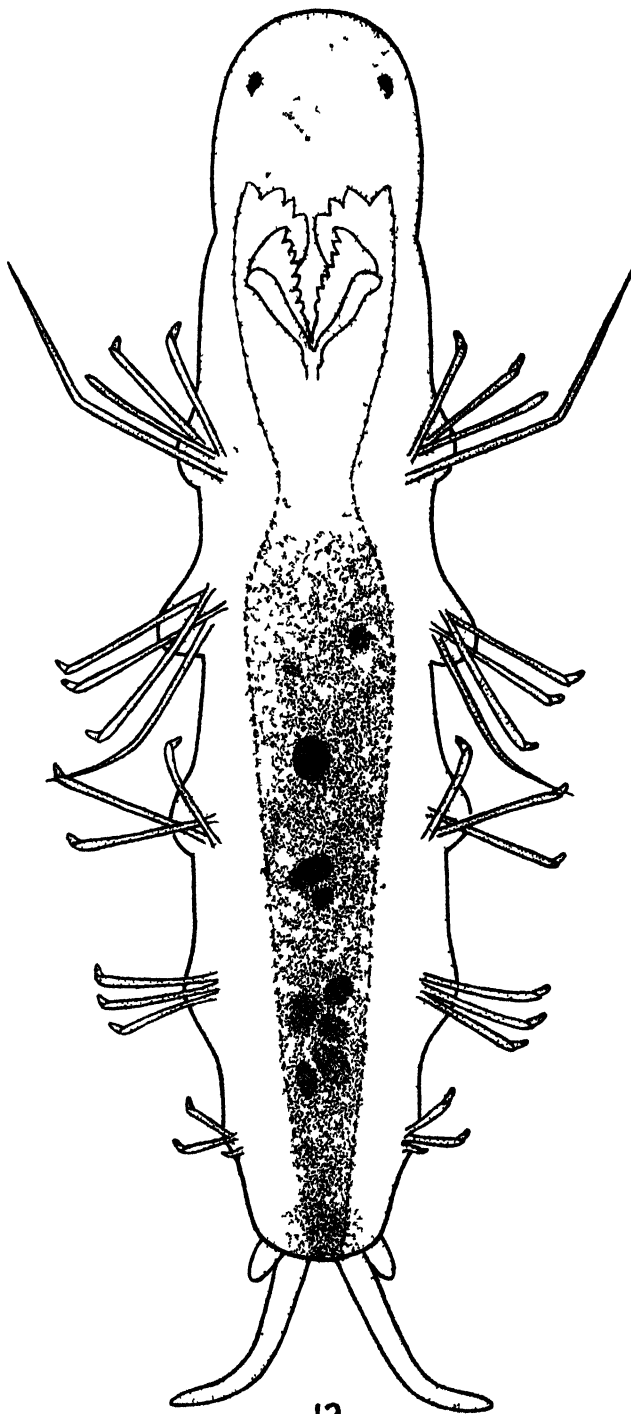
Corresponding to a fully developed Nectochæta. Cilia absent. Rudiments of jaws, three pairs of setose tufts, and two pairs of anal styles are present. $\times 350$.

his "Studies on Polychæte Larvæ," says, "In the Nereidiformia and some other worms there usually develop during the Metatrochophore stage a number of segments, definite for each species, all of which appear at about the same time and whose parapodia become very fully developed before any further segments are added; the former, including the peristomial and excluding the anal, are called primary, the latter secondary segments." In the present form there is no such precocious development of the appendages of any of the first-formed segments, and consequently a distinction between primary and secondary segments does not seem to exist.

The alimentary canal becomes elongated ; it remains clear in the pharyngeal region, in which a pair of chitinous toothed plates—the second maxillæ—appear. These are soon followed by the elongated mandibles, but the other parts of the dental apparatus are not distinguishable as yet. A second pair of anal styles external to those already present are developed at this stage. The larva (text-fig. 10) has now reached a stage corresponding to the *Nectochæta* stage of Hacker, who (6) describes it thus in his “*Pelagische Polychætenlarven*” : “*Halbkugelförmige Umbrella: zweizeiliger Prototroch; zwei Augenfleckpaare: zunächst drei Paare Parapodien, bestehend aus einem grossen flossenförmigen ventralen Ast mit Borstenbündel und ventral Cirrus, sowie aus einem dorsalen Cirrus; unpaare Scheitel-Cirrus, ein Paar Fühler-Cirren, zwei Paar After-Cirren.*” The description given and the diagram figured for the *Nectochæta* of the Naples species are very different from the corresponding stage in the present form. In Hacker's form the three pairs of appendages have attained a considerable degree of specialization. There are oar-shaped fleshy parapodial lobes from which bundles of jointed setæ (6 in the first, 4 in the second, and 5 in the third) spring. Dorsal and ventral cirri, an unpaired apical cirrus, a pair of dorsal tentacular cirri, and a pair of anal cirri are present. Two pairs of eyes and two narrow ciliated bands are also present.

In the corresponding stage of the present form, the setose parapodial tufts start almost directly from the body, there being no basal flattened fleshy processes. There are never more than three jointed setæ in the second and third pairs of tufts, and four setæ in the first, of which one at least is always unjointed. A single pair of eyes alone are present (almost black with a slight reddish tinge), and as yet there is no indication of dorsal and ventral cirri. Cilia and ciliated bands are completely absent. The larvæ, unlike those of the Naples form, are altogether incapable of swimming and remain creeping at the bottom of the glass. This is obviously an adaptation to development in a jelly.

Prostomium, Eyes, and Cirri.—The prostomium is rounded, and does not exhibit at this stage that bifid condition which is so characteristic of the adult Eunicid. The pharyngeal region remains clear, but the rest of the digestive canal often exhibits a yellowish-green colour on account of the material in the gut (text-fig. 12). The creeping habit is given up as new segments begin to be added, and the tiny worms construct small tubes formed mainly of organic debris cemented together by mucus secreted by the skin. New segments are added in front of the anal segment, and the newly formed setæ are usually of the jointed variety. When 8–10 segments with their appendages have been differentiated, the dorsal cirri make their appearance in the form of small almost transparent fleshy tubercles. The ventral cirri appear later. The larval eyes become gradually reduced, and when 13–14 chaetigerous segments have been formed they are almost gone. Their place now is taken by the adult eyes, which appear in the position afterwards occupied by the future intermediate tentacles. At this stage the young worm is provided with two pairs of eyes—the anterior pair gradually diminishing, the posterior gradually becoming bigger.



12

A tiny worm with five setigerous segments. In the last two or three segments only hooked compound setae are present. $\times 350$,

Setæ.—Meanwhile, the number of setæ in the chaetigerous tufts of the anterior segments has increased, and three kinds of setæ may now be distinguished :—

1. Unjointed capillary setæ characteristically bent and taking up a more and more dorsal position (text-fig. 13).
2. Jointed setæ of the hooked variety with a short terminal hooked blade, the basal shaft being slightly dilated and pointed at the end (text-fig. 14).
3. Jointed setæ with moderately long sickle-shaped blade (text-fig. 15), approximating to the falcigerous type. The second and third varieties have a more ventral position than the first.

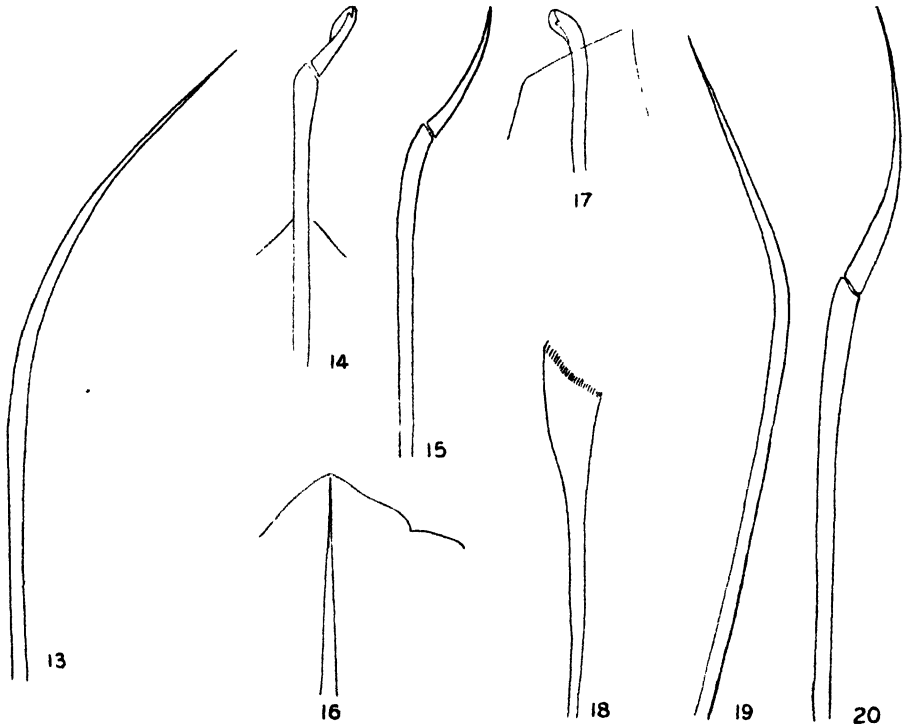


Fig. 13.—A capillary seta of a worm with seven pairs of appendages. $\times 700$.

Fig. 14.—A hooked seta of the same worm. $\times 700$.

Fig. 15.—Falcigerous seta of worm with 13 pairs of appendages. $\times 700$.

Fig. 16.—An aciculus from the same worm. $\times 700$.

Fig. 17.—An acicular seta, bent, with guard and hook, of the same worm. $\times 700$.

Fig. 18.—A comb-seta from the posterior end of worm with more than 100 segments. $\times 700$.

Fig. 19.—A capillary seta from the same worm. $\times 700$.

Fig. 20.—A falcigerous seta from a worm with more than 100 segments. $\times 700$.

Beside these, acicula (text-fig. 16) and acicular setæ (text-fig. 17) are developed when the worm is provided with 12 to 14 pairs of appendages. The former appear in the first few anterior segments, the latter at about the same

time in the posterior and are absent in the anterior segments. The comb-setæ (text-fig. 18) also appear at about this time. In worms with 70–80 chætigerous segments capillary and falcigerous setæ are found in the anterior segments, while all three kinds of setæ are represented in the posterior. The hind segments still continue to form hooked and capillary setæ. At a fairly late stage, in worms with more than 150 segments, the formation of hooked setæ in the newly-forming posterior segments is gradually given up; only capillary setæ are developed in these. Thus worms of more than 150 segments have capillary and falcigerous setæ in the greater part of the body and only capillary setæ in the posterior segments.

An examination of the parapodia of very young worms of different ages shows a series of transition-stages. The text-figs 21–29 show clearly the facts set forth above.

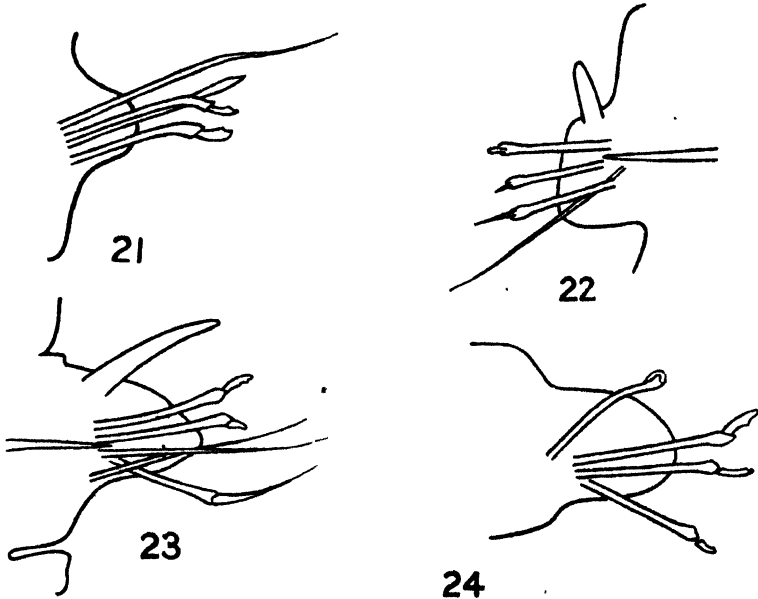


Fig. 21.—1st right parapodium of a worm with 7 pairs of appendages. $\times 350$.

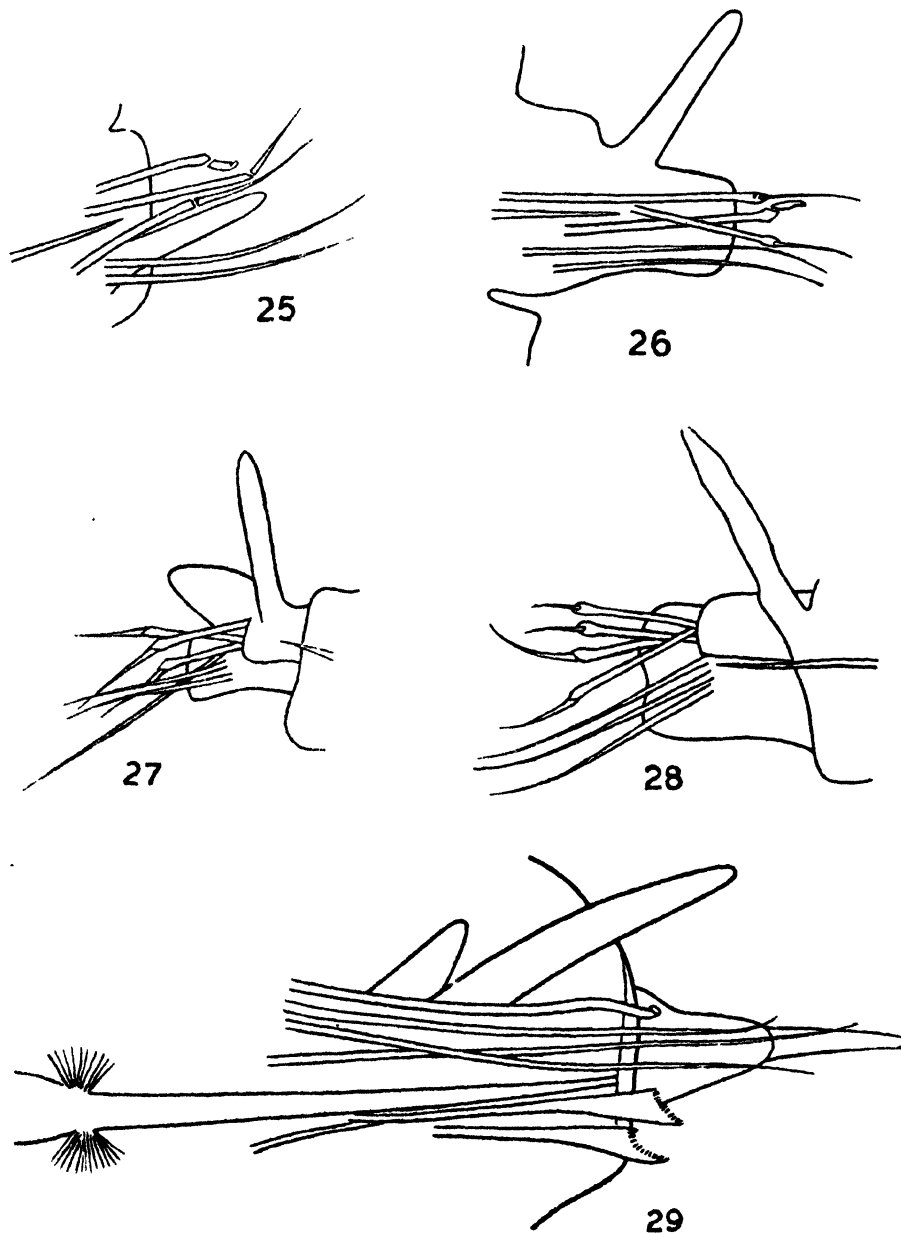
Fig. 22.—1st left parapodium of a worm with 16 pairs of appendages. $\times 350$.

Fig. 23.—5th right parapodium of the same worm. $\times 350$.

Fig. 24.—15th right parapodium of the same worm. $\times 175$.

Text-fig. 21, the right setose tuft of a worm with seven pairs of appendages, shows three jointed setæ of the hooked variety, one capillary seta, and no setæ of the falcigerous kind.

Text-figs. 22 and 23 show the 1st left parapodium and the 5th right parapodium of a worm with 16 pairs of tufts, both provided with dorsal cirrus, aciculum, and setæ of all the types; while text-fig. 24 shows the right parapodium of the 15th chætigerous segment, without dorsal cirrus and aciculum, but possessing an acicular seta with guard and three jointed setæ of the hooked variety.



Figs. 25 & 26.—The first and fifth parapodia of a worm with 25 pairs of parapodia and their tentacles. $\times 175$.

Figs. 27 & 28.—The first and fifth parapodia of a worm with 60 setigerous segments. $\times 175$.

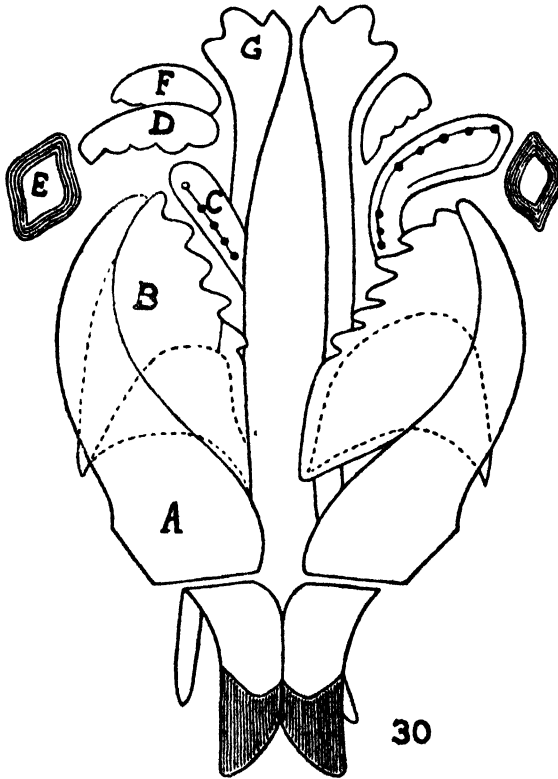
Fig. 29.—A right parapodium from the posterior end of a worm with about 175 chaetigerous segments. $\times 175$.

(Figs. 21–29 from dorsal aspect under coverslip.)

In text-figs. 25 and 26, representing the right parapodium of chaetigerous segments 1 and 5 of a worm with 25 pairs of appendages, all three kinds of setae are seen to be present.

In text-figs. 27 and 28, which represent the parapodia of chaetigerous segments 1 and 5 of a worm with more than 60 pairs of appendages, all the hooked setae have been replaced by sickle-shaped ones. Text-fig. 29, a parapodium from the extreme posterior end of a worm with more than 150 segments, shows no jointed setae at all.

The final condition of the setae is thus arrived at rather late, and it becomes a question of how far descriptions of setae based on the examination of small worms can be of specific value.

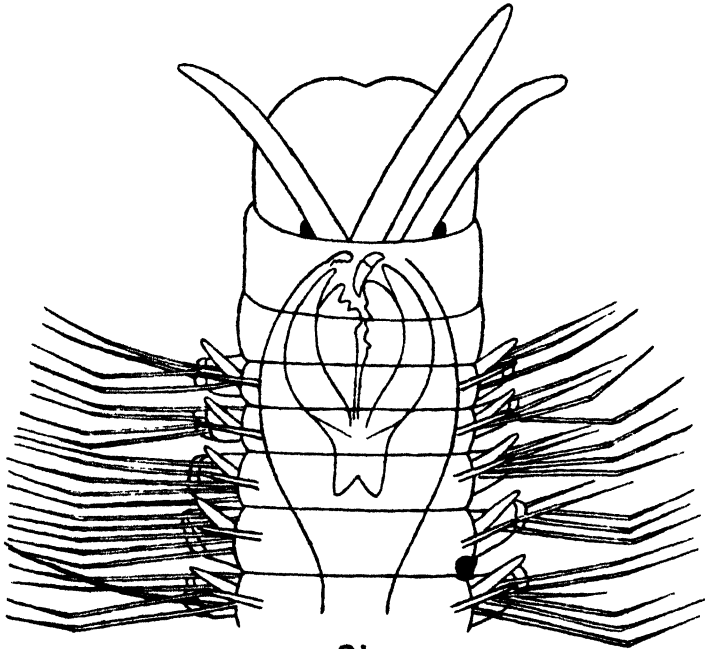


Dental apparatus of young worm with 25 pairs of appendages. A. Forceps jaw ; B. 2nd maxilla ; C. 3rd maxilla ; D. 4th maxilla ; E. 5th maxilla ; F. Additional plate ; G. Mandible. $\times 40$.

Jaws begin to appear as early as the stage which corresponds to the Necto-chæta, and the full complement of parts is reached by the time that 8-10 pairs of appendages have been formed. When fully formed the entire jaw apparatus consists of the following (text-fig. 30) :—

1. A pair of ventrally placed mandibles, long, slender, and diverging posteriorly, broad and united anteriorly, with three big obtuse teeth.

2. A pair of forceps jaws, each of two pieces, the basal pieces united by the greater part of their length and black behind. The distal pieces are robust, bluntly pointed, moderately curved, and black at the tips. No teeth are present. The proximal pieces are cut off obliquely at their bases, so that a notch is formed between the two apposed pieces at the posterior end.
3. The second pair of maxillæ (grinders) are massive and provided with five black teeth on the left and six on the right side.
4. The third pair of maxillæ are in the form of crescentic plates, the right being the bigger and placed slightly in advance of that on the left side, both being marked by a ridge and elevated into 8-9 small tubercles on the right and 5-6 bigger ones on the left.



31

Anterior end of a worm with 60 setigerous segments, three tentacles, and a pair of eyes. Only capillary and falcigerous setæ are present in the anterior segments. $\times 40$.

(All drawings made from fresh preparations.)

The number of teeth in the second and third pairs of maxillæ is subject to great variation. They are more numerous in the younger than in the adult stages.

5. The fourth pair of maxillæ are irregular with four indistinct teeth on each, the teeth on the right side being much less conspicuous than those on the left.
6. The fifth pair of maxillæ are in the form of rhomboidal plates elevated all round into a ridge. Teeth are absent.

On the left side there is in addition another piece, toothless and unrepresented on the right side.

Gills arise in worms with 15–16 pairs of appendages as single filaments from the dorsal cirrus of the 8th or 9th pedigerous segment. The full number of filaments and pectinate shape are attained gradually as more segments are added.

Tentacles.—The median tentacle appears for the first time when the worm is provided with 18–20 segments, grows rapidly, and two days later is followed by the intermediate tentacles. The lateral tentacles develop very late, only when more than 80 pairs of appendages have been formed.

This late development of the tentacles is in marked contrast with their early development in the Nectochæta of the Naples species and other Nectochæta larvæ described by Gravely for other families of the Nereidiformia.

The worms reared in the laboratory from the spawn-masses are exactly like the worms dug out from the soil where the pear-shaped masses of spawn abound, except in their smaller size and in the smaller number of filaments in each gill. It takes nearly six months for a worm to develop 150 to 180 segments and the gills to acquire 5–6 filaments. Judging from this the worms dug out from their natural habitat, sometimes measuring up to 18 inches or more and possessing about 750 segments, are probably 3–4 years old at the least.

Borradaile (7) describes the initial development of a species of *Marphysa* (*teretiuscula* ?) with which the development of the present form very closely agrees. His account, however, extends only up to the formation of the fourth setiger, and the few minor differences are what one would expect in two different species of the same genus. Dr. Southern* mentions similar spawn-masses as being formed by *M. graveleyi* from the Chilka Lake and figures an early stage (12), Herpin (15) traces the development of *Eunice harassii* to a much later stage, and a comparison of the development of present form with that of *E. harassii* is highly instructive.

In *E. harassii* the eggs are not laid in a jelly, and this seems to be the reason for the many differences in the details of development. Here there is a well-marked pelagic phase lasting for over ten days, during which the larva seems to be engaged in parapodial differentiation rather than in the quick formation of new setigers. At the close of the pelagic phase the fourth setiger has appeared and the first already possesses a dorsal and a ventral cirrus, and by the twelfth day the second is also equipped in a similar manner. The larva passes in succession through what Herpin calls the "Nematonereis," "Lysidice," and "Amphiro" stages, characterized respectively by (i) a median tentacle, (ii) median and intermediate tentacles and absence of branchiæ, (iii) median and intermediate tentacles and simple branchiæ with absence of pectinate setæ. Development is very slow, being characterized by rapid differentiation of existing parts rather than by the addition of new setigers. Thus at the Nematonereis stage, which is reached in fourteen days there, is a median

* The Madras form was submitted to Dr. Southern, and he considers it to be different from *M. graveleyi*.

tentacle and five setigers only. The Lysidice stage is reached in three months and the larva is provided with three tentacles and 13 setigers, and at the Amphiro stage, which takes ten months to reach, 3 tentacles, 20 setigers, and simple branchiæ have appeared.

From what has been said it will be seen that it is not possible to apply the terms Nematonereis, Lysidice, and Amphiro to the stages of development of the present form, for here we have in the course of development a curious overlapping of characters and an absence of that orderly process so characteristic of *E. harassii*.

Unlike *Staurocephalus*, the definitive pair of eyes, as in *E. harassii*, are the posterior ones.

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Report on the Crustacea Brachyura of the Percy Sladen Trust Expedition to the Abrolhos Islands under the Leadership of Professor W. J. DAKIN, D.Sc., F.L.S., in 1913; along with other Crabs from Western Australia. By STEPHEN K. MONTGOMERY, B.A., B.Sc., M.D., B.S., M.R.C.S., L.R.C.P., F.L.S.

(PLATES 24 30, and 1 Text-fig.)

[Read 21st November, 1929.]

THE collection which is the subject of this report was made at the Abrolhos Islands, off Geraldton, Western Australia, by the Percy Sladen Trust Expedition under the leadership of Professor W. J. Dakin, D.Sc., in November 1913. In addition there are specimens from Broome, the Swan River near Perth, the coast near Fremantle, and Albany.

The collection consists of 248 specimens, 192 of which are from the Abrolhos, and contains 55 species two of which show distinct varieties: of these 42 species occur at the Abrolhos, one of which is represented by two varieties. Eight new species are described, 6 of them from the Abrolhos, and 4 new varieties, 3 from the Abrolhos. For one of the new species a new genus is set up. Nine species beside the new species are new to the Australian fauna, and 14 others new to Western Australia. In the list of species in the collection subjoined, those not found at the Abrolhos are marked with an asterisk (*), those new to Australia (other than new species) with a dagger (†), and those new to Western Australia by an exclamation mark (!).

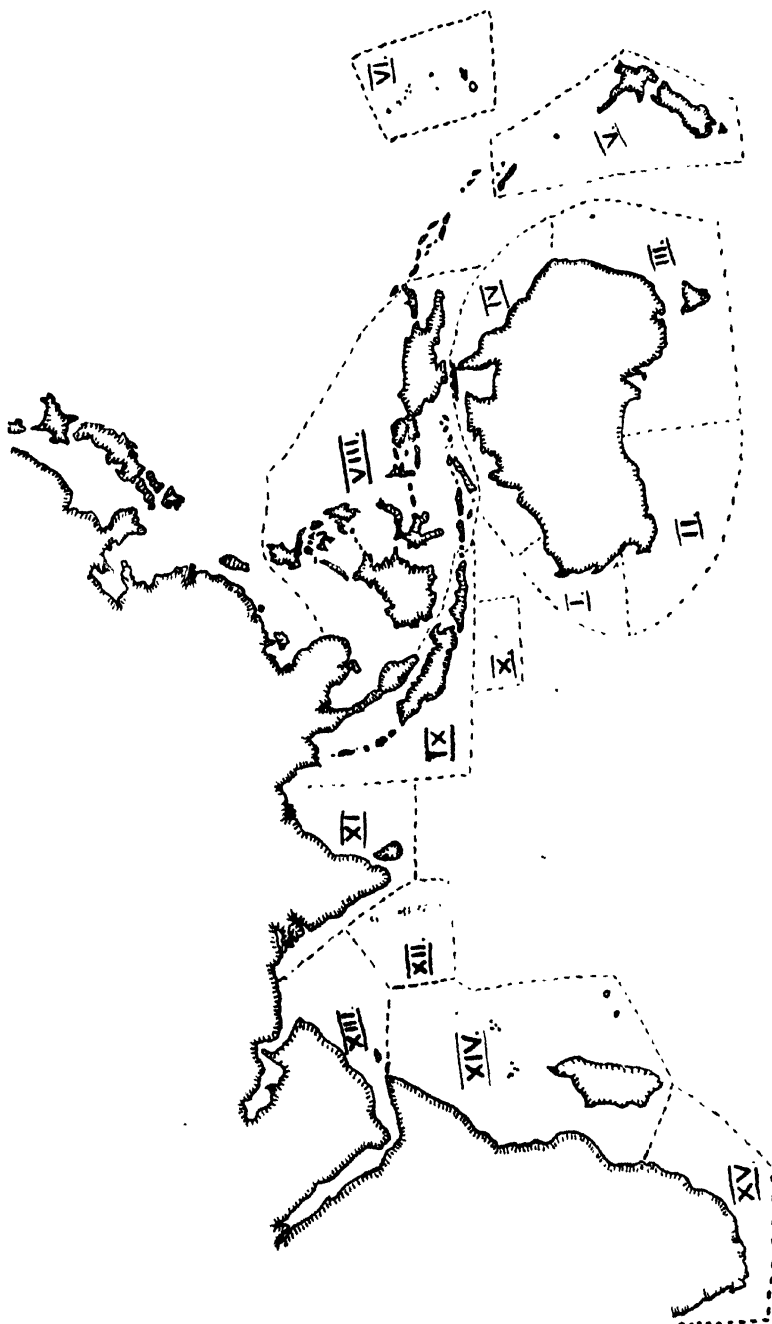
LIST OF SPECIES.

1. *Cryptodromia tumida* Stimpson, 1859 †.
- 1 a. ——— var. *spinifera*, var. n.*.
2. *Dromidiopsis abrolhensis*, sp. n.
3. *Ephippias endeavouri* Rathbun, 1918.
4. *Huenia proteus* de Haan, 1839 *.
5. *Menæthus monoceros* Latreille, 1825.
6. *Paranaxia serpulifera* Guérin-Méneville, 1834 (?).
7. *Cyclax* (*Cyclomaia*) *suborbicularis* Stimpson, 1858.
8. *Schizophrys dama* Herbst, 1804.
9. *Micippa philyra* Herbst, 1803.
10. *Naxia aurita* Latreille, 1825 !.
11. *Halicarinus australis* Haswell, 1882 b *.
12. ——— *bedfordi*, sp. n.*.
13. *Elamena truncata* Stimpson, 1859 !.
14. *Portunus pelagicus* Linnæus, 1758.

15. *Thalamita prymna* (Herbst, 1803) var. *pelsarti*, var. n.
- 15 a. ——— var. *proxima*, var. n.
16. ——— *sima* Milne-Edwards, 1834.
17. ——— *macropus*, sp. n.
18. ——— *dakini*, sp. n.
19. *Kraussia hendersoni* Rathbun, 1902 †.
20. *Liomera cinctimana* White, 1847 a !.
21. ——— *bella* Dana, 1852.
22. *Lophozozymus pulchellus* A. Milne-Edwards, 1867 †.
23. *Xantho impressus* Lamarck, 1818 †.
24. ——— *hydrophilus* Herbst, 1790.
25. *Actæa helleri* A. Milne-Edwards, 1865 a !.
26. ——— *calculosa* Milne-Edwards, 1834.
27. ——— *savignyi* Milne-Edwards, 1834 *.
28. ——— *depressa* (White, 1847 b) var. *abiohensis*, var. n. †.
29. ——— *rufopunctata* Milne-Edwards, 1834 †.
30. ——— *lvidorsalis*, sp. n.
31. *Parazanthias elegans* Stimpson, 1859.
32. *Chlorodiella nigra* Forskal, 1775.
33. *Phymodius unguatus* H. Milne-Edwards, 1834.
34. *Chlorodopsis areolata* H. Milne-Edwards, 1834.
35. *Ozius truncatus* H. Milne-Edwards, 1834 !.
36. *Pilumnus contrarius* Rathbun, 1923 * !.
37. ——— *digitalis* Rathbun, 1923 !.
38. ——— *edamensis* de Man, 1888 b †.
39. ——— *pulcher* Miers, 1884 * !.
40. ——— *semilanatus* Miers, 1884 * !.
41. ——— *spinicarpus* Grant & McCulloch, 1906 * !.
42. ——— *granti*, sp. n.
43. ——— *maccullochi*, sp. n.
44. *Actumnus obesus* Dana, 1852 a †.
45. *Litochira bispinosa* Kinahan, 1856 *.
46. *Pinnotheres edwardsi* de Man, 1888 a †.
47. *Ocypode pygioides* Ortmann, 1894 b.
48. *Leptograpsus variegatus* Fabricius, 1775.
49. *Leptograpsodes*, gen. n., *webhaysi*, sp. n.
50. *Planes minutus* Linnæus, 1758 *.
51. *Cyclograpsus audouinii* H. Milne-Edwards, 1837 * !.
52. *Percnon planissimum* Herbst, 1804.
53. *Plagusia capensis* de Haan, 1835 * !.
54. ——— *depressa* (Fabricius, 1775) var. *tuberculata* Lamarck, 1818.
55. Corystoid gen. et sp. indetermin.

The knowledge of the crabs of the West Australian coast is relatively scanty : for example, among the species described as new to Western Australia, two, *Plagusia capensis* de Haan, 1835, and *Cyclograpsus audouinii* Milne-Edwards, 1837, are quite common and of everyday occurrence, while another, *Ocypode pygioides* Ortmann, 1894 b, occurs literally in tens of thousands, though it has never been reported since Ortmann's original description.

As a foundation to the present work W. A. Haswell's 'Catalogue of Australian Malacostraca,' 1882, has been taken ; the main additions to the Australian



Sketch-map of Indo-Pacific Region, showing arbitrary divisions.

Brachyuran fauna since then have been made by the work of T. Whitelegge, A. R. McCulloch, and F. A. McNeill in New South Wales, S. W. Fulton and F. E. Grant in Victoria, and W. H. Baker in South Australia; by E. J. Miers in his 'Alert' and 'Challenger' reports, A. Ortmann, W. T. Calman, and M. J. Rathbun, the four recent papers of the last-named on Australian crustacea being most useful. As in all work on the Indo-Pacific fauna A. Alcock's 'Materials for a Carcinological Fauna of India' is essential, and much assistance has been derived from the works of J. G. de Man, H. Balss, L. A. Borradaile, and R. D. Laurie, the latter's Red Sea report being of great use from the point of view of geographical distribution. T. R. R. Stebbing's South African Crustacea and the 'Siboga' reports of J. E. W. Ihle and J. J. Tesch have been of great use for synonymies. A full list of the literature cited is appended at the end of the paper.

In order to assign the Abrolhos Brachyura their proper place in the Indo-Pacific fauna, it is necessary to compare them with the Australian fauna as a whole.

For purposes of discussion of the distribution of the Brachyura the Indo-Pacific has been divided arbitrarily into districts as shown in the sketch-map on p. 407.

The list of Australian Brachyura shows 508 species, and 23 varieties in addition. It is found that 89 species have been reported from the North-West district, which has been taken to range from just south of Geraldton to the southern end of the Ninety-Mile Beach, south of Broome. Of these, 42 species are in the Abrolhos collection; the only species of which previous record from the Abrolhos has been found is *Cyclax (Cyclomaia) suborbicularis* Stimpson, 1857, by Haswell in his Catalogue. Of these 42 species, 13 have been found both on the Islands and elsewhere in the north-west district; 23 are common to the northern district and 19 common to the southern. In estimating the relations of the Abrolhos with other districts, account must be taken of the large numbers of extremely widespread forms which are common practically to the whole of the Indo-Pacific; thus of the 23 forms common to the Abrolhos and the northern district, 15 occur also in the southern district and 12 elsewhere in the north-west; and, in order to affirm that the Abrolhos Crabs show a predominantly tropical or a predominantly temperate facies, this factor must be borne in mind. Of the nine species in the collection which are new to Australia, all are from the Abrolhos, two occur also in the northern district (one being varietally distinct), and all are tropical. If one neglects the common factor of 15 almost universal species common both to north and south, there are, therefore $(23 - 15) + 9 = 17$ out of $(42 - 15) = 27$ species of northern or tropical distribution at the Abrolhos and $(19 - 15) = 4$ of southern. There is, therefore, a distinct tropical bias among the Abrolhos Crabs.

The homogeneity of the Indo-Pacific Brachyuran fauna has been stressed by Laurie, 1915. His conclusion is that "the Indo-Pacific figures suggest that one may prophesy with a probable error of ± 5 or 6 that 35 is the most

likely percentage of species common to the Red Sea which will be found in a collection of, say, 200 species of crabs from any hitherto insufficiently explored portion of the Indo-Pacific region." The Australian fauna is not altogether consistent with his findings; the southern fauna is definitely not comparable with the rest of the Indo-Pacific faunas, and even the northern shows less relation than Laurie's average; the north-west fauna alone approaches Laurie's 35 per cent. of crabs common to the Red Sea.

For purposes of comparison, Laurie's complete list of Red Sea Crabs has been taken and the percentage of Australian Crabs occurring in it has been shown in Table I (p. 410). Table II shows the distribution in Australia of the species which occur in more than one district.

It will be noted that the different families of crabs vary considerably in the "percentage of homogeneity"; this may be noted also in Laurie's table. The Portunids, as might be expected, are above the average, and the Xanthids are the next most widespread. It may be remarked, too, that it is the extremely widespread species, occurring in all Australian districts, which bring the "percentage of homogeneity" up; this may be inferred in Table I from the fact that, where one considers species in the Australian fauna occurring only in one particular district, the percentage of forms common to the Red Sea is almost invariably much lower than when one considers all the forms of that district.

It seems that in general the distribution of the crabs falls into three classes—local, focal, and general. In many cases there are local varieties of a species of generalized distribution as in the case of the *Thalamita prymna* series, or *Actaea peroni* var. *occidentalis* (Odhner, 1925); certain species of *Pilumnus* tend to be very local in their distribution. Other species appear to be more widespread round some focus, usually, in the case of the Indo-Pacific Crabs, somewhere about the western side of the Malay Peninsula, or else more easterly among the Pacific Islands; *Xantho impressus* (Lamarck, 1818) exemplifies the former, and perhaps *Pilumnus vestitus* (Haswell, 1882 b) the latter. The generalized forms are quite 20 per cent. of the total; Laurie's figure, 35 per cent. of any Indo-Pacific collection common to the Red Sea, is too high for the Australian fauna, and is very largely made up, in any particular case, of these generalized forms.

Perhaps the most striking example of the focal distribution is shown by the Oxystomata; 26 out of 65 Australian forms are not found elsewhere. Of the rest, quite a large majority are found roughly in the distribution—East Indies, India, Ceylon, and the Maldive Islands; a few are generalized and a few show other areas of distribution; in support of the view that the Oxystomata have spread from a Malayan focus, it is worth remark that only 65 Oxystomes out of 506 species occur in the Australian fauna, whereas in Alcock's 'Carcinological Fauna of India' 113 occur out of 601 species; further, the number of Oxystome species in Australia grows progressively less as one goes farther from

TABLE I.—Showing Percentage of Australian Species of each Family common to the Red Sea.

	Total Australian species.	Number common to Red Sea.	Percentage common to Red Sea.	Australian species only in northern district.	Number common to Red Sea.	Percentage.	Total species in northern district.	Number common to Red Sea.	Percentage.	Australian species only in southern district.	Number common to Red Sea.	Percentage.	Total species in southern district.	Number common to Red Sea.	Percentage.	Australian species only in north-west district.	Number common to Red Sea.	Percentage.	Total species in north-west district.	Number common to Red Sea.	Percentage.
Dromiidae	24	0	0	7	0	0	9	0	0	13	0	0	15	0	0	2	0	0	2	0	0
Oxytomata	66	11	17	31	6	19	44	9	20	17	1	6	30	5	17	3	0	0	9	2	22
Oxyrhyncha	110	14	13	50	7	14	72	14	19	35	0	0	52	3	6	1	0	0	15	5	33
Portunidae	39	16	41	18	6	33	24	11	46	11	2	18	17	8	47	4	0	0	9	3	33
Xanthidae	142	43	30	75	20	27	111	39	35	16	2	12	45	16	36	13	2	15	35	15	43
Goneplacidae	16	0	0	6	0	0	11	0	0	5	0	0	10	0	0	0	0	0	0	0	0
Pinnotheridae	11	0	0	4	0	0	5	0	0	5	0	0	6	0	0	1	0	0	1	0	0
Grapsoidae	71	15	21	14	3	21	34	12	35	30	2	7	50	11	22	6	0	0	15	5	33
Palicidae	4	2	50	4	2	50	4	2	50	0	0	0	0	0	0	0	0	0	0	0	0
Haplocarcinidae	2	1	50	2	1	50	2	1	50	0	0	0	0	0	0	0	0	0	0	0	0
Hymenosomidae	11	0	0	0	0	0	1	0	0	9	0	0	11	0	0	0	0	0	1	0	0
Corystoidea	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichiidae	3	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0
Potamonidae	5	0	0	4	0	0	5	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Mictyridae	3	0	0	1	0	0	2	0	0	1	0	0	2	0	0	0	0	0	1	0	0
	508	102	20	218	47	21	326	92	28	143	7	5	240	43	18	31	2	6	89	30	34

TABLE II.—Showing Distribution in various Districts of Australia.

Districts.	Dromidae.	Oxyrhyncha.	Portunidae.	Xanthidae.	Gonophoridae.	Pinnotheridae.	Grapsoidea.	Palicidae.	Hapalocarcinidae.	Hymenosomidae.	Trichidae.	Potamonidae.	Mictyridae.	Corystoidea.
N.+S.E.	1	9	1	13	4	1	12	1	..	51
N.+S.W.	1	1	2
N.+N.W.	2	7	9	1	19
S.E.+S.W.	1	1	8	1	1	..	2	1	15
S.E.+N.W.	2	1	2	1	1	7
S.W.+N.W.
N.+S.E.+S.W.	1	2	1	1	5
N.+S.E.+N.W.	2	3	9	3	19
N.+S.W.+N.W.	1	1
S.E.+S.W.+N.W.	1	1
N.+S.E.+S.W.+N.W.	2	3	2	3	1	..	11
Total														131
N. = Northern district.														
S.E. = South-eastern district.														
S.W. = South-western district.														
N.W. = North-western district.														
N. only														218
S. only														143
N.W. only														31
Less S.E.+S.W. (included in S. only) ..														523
Total species														508

Cape York and Northern Australia ; 44 of the 65 are northern, 29 southern, and 9 north-western. Of the southern species 3 only occur in the south-west—*Merocryptus lambriformis* (A. Milne-Edwards, 1873 b) at Eucla, *Philyra globosa* (Fabricius, 1798) at Fremantle, and *Philyra lævis* (Bell, 1855) at Albany. At the Abrolhos, no representative of the group has been recorded.

Another notable absentee from the Abrolhos is the genus *Sesarina* (Say) ; the species of this genus may possibly also have spread from a Malayan focus ; of the eight Australian species, all are from the north or the east of Australia, and none occur among the fourteen Mergui specimens of de Man, 1888 ; the genus is probably in a rather fluid evolutionary state, and different variations have adapted themselves as species in different localities as it has spread south.

It will be observed that the Ninety-Mile Beach, south of Broome, has been taken as the northerly limit of the north-western district ; the collections are not yet sufficiently complete for a definite opinion, but it seems probable that this will turn out to be a true "zoological barrier." At present, 20 species are known to occur in Western Australia both north and south of the beach, 52 are confined to the north, up to the Holothuria Bank and King's Sound, and 88 to the south, as far as Eucla. By comparison, of the 72 species from the north, 50 occur elsewhere in the North of Australia, and 22 only are confined to the west ; while of the 20 West Australian species which are common to districts north and south of the Ninety-Mile Beach, all are found elsewhere in the north of Australia.

The author's best thanks are due and are gratefully recorded to Professor W. J. Dakin for having placed the collection at his disposal, and for having given him both the stimulus and opportunity to undertake the work ; to Dr. W. T. Calman, who has given him access to the collections in the keeping of the British Museum (Natural History), and has been ever ready both with helpful advice and criticism and the loan of literature ; to Dr. J. G. de Man and Professor Ch. Gravier for assistance with regard to synonymies and the loan of a very valuable specimen ; to Miss F. R. Mold for her careful work in preparation of the figures ; and to the Library staffs at South Kensington, who most assiduously helped in a long and arduous check of the literature. I must also record my indebtedness to the Trustees of the Dixon Fund of the University of London, both for a very munificent grant in aid of publication, and also for great forbearance in their demands for the completion of the work.

The following is the annotated list of species in the collection. All measurements are in millimetres, unless otherwise stated. The abbreviations are : C.=Carapace, l=length, b=breadth, W.-L.=Walking-leg, Ch.=cheliped, R.=Rostrum. In the distributional lists the figures in brackets refer to the serial numbers in the list of publications cited.

The teeth, whether rostral, supraorbital, infraorbital, or subhepatic, are much more strongly developed, and the ridges and knobs more marked than in the typical *C. tumida*. The antero-lateral teeth are three on the right side, only two on the left, the middle one being represented by a slight sinuosity only. There is no epipodite on the chelipeds (*i. e.*, it is a true *Cryptodromia*, *vide* Borradaile, 1903 c), but otherwise it strongly resembles *Paradromia lateralis* (Gray, 1831) [*vide* Balss, 1921], if the left antero-lateral border is taken as typical and the right as aberrant. The first tooth of the antero-lateral border, which is the outer orbital angle, and the second tooth are so strongly marked as to obscure the stout subhepatic tooth from dorsal view; the eyes also are not visible from above.

The propodite of the last pair of legs bears four sharp spines at its distal end surrounding the base of the sharp curved dactylus; two spines are behind the dactylus, two in front.

The sternal ridges are peculiar, ending wide apart on the level of the coxa of the first pair of legs, not in a small mound as in the typical *C. tumida*, but in a transverse ridge.

These characters may be simply those of immaturity, and one hesitates to separate a distinct species; nevertheless, it is significant that this specimen is the only one in the collection from outside the Abrolhos Islands, where the typical species is abundant.

Distribution.—Broome.

2. *DROMIDIOPSIS ABROLHENSIS*, sp. n. (Pl. 25. fig. 4; Pl. 30. figs. 1, 1 a, 1 b, 1 c.)

Locality.—1 ♀, Coral Flats, East Wallaby Island.

Measurements (in mm.) :—

C. l.	43
C. b.	43
W.-L. 5 l.	45 (23+22)
W.-L. 4 l.	33 (16+17)
W.-L. 3 l.	53 (23+30)
Propodite W.-L. 5 l.	8
„ „ b.	5

This species is closely allied to *D. edwardsi* (Rathbun) [= *D. caput-mortuum* (Milne-Edwards, *nec* Linnaeus), *vide* Rathbun, 1919, p. 195], and to *D. cranioides* (de Man, 1888 b, p. 208) and *D. australiensis* (Haswell, 1882 b), which is redescribed by de Man, 1888 b, p. 396, pl. xvii, fig. 6; Ihle, 1913, p. 26.

In *D. abrolhensis* (i) the lateral teeth (Pl. 30. fig. 1, a) of the front are sharper and more prominent than in *D. edwardsi*, and the middle tooth (fig. 1 a, b) is extremely small, is downwardly directed, and, arising as it does from a plane posterior to the roots of the lateral teeth, is entirely invisible from dorsal view; the front is broader than in *D. edwardsi*, narrower than in *D. australiensis*, and is cleft much deeper than in the latter; (ii) the supra-orbital border is more prominent than in *D. edwardsi*, is not spined “with an acuminate tooth”

as in *D. cranioides* (Alcock, 1899 *b*), but projects as a sinuous rounded edge (Pl. 30. fig. 1, *c*) ; the front is separated from the supraorbital border by a fairly deep bay (fig. 1, *d*), much deeper than the "slight baying out" of *D. australiensis* ; (iii) owing to the prominence of the supraorbital border and of the antero-lateral teeth, there is a distinct bay (fig. 1, *e*) between the latter and the outer orbital angle (fig. 1, *g*), not a gentle curve as in *D. edwardsi* ; (iv) the fissure separating the infraorbital from the supraorbital border is fairly deep, not "a tiny linear fissure" as in *D. australiensis* or "small fissure" as in *D. edwardsi* ; (v) the infraorbital border has a distinctly separate tooth (fig. 1 *a*, *f*) as in *D. cranioides* and *D. australiensis*, and unlike *D. edwardsi*, but it is rounded off, not spined ; (vi) the teeth of the antero-lateral border are four in number, excluding the outer orbital angle ; they are sharper than in *D. edwardsi* and *D. australiensis*, but not so prominent as in *D. cranioides* ; the third (fig. 1, *k*) and fourth (fig. 1, *l*) are larger than the second (fig. 1, *j*), which is quite rudimentary and is barely to be distinguished arising from the lateral aspect of the first (fig. 1, *h*). The interval between the first tooth and the third tooth is greater than that between the third tooth and the branchial grooves, not, as in *D. cranioides*, equal to it. The first tooth is not transversely truncated, as in *D. edwardsi*, but is pointed ; (vii) the prominence of the frontal teeth and antero-lateral teeth causes the general outline of the fronto-orbital region, in front of a line joining the first antero-lateral teeth, to be trapezoid, not semicircular as in de Man's figure of *D. edwardsi* (*ridé de Man*, 1888 *b*, pl. xvii, fig. 5) ; (viii) the chelipeds are equal ; the merus has some very small teeth on two borders only, there being five and a rudiment on the upper border ; on the carpus, there are no teeth on the upper border, except at the distal end which has the form of a small blunted tooth ; the hand has, on the upper border, four small indistinct tubercles, the middle two being the largest, but no teeth (as compared with *D. edwardsi*, which has two teeth, and *D. cranioides*, which has three) ; the chelipeds are stout and covered with tomentum which extends to the base of the fingers, and, in certain parts, along them toward the point. On the outer side of each finger is a deep pointed groove filled with tomentum. In the mobile finger the upper border of this groove is continuous through the apical tooth of the finger with the inner margin of the finger. The lower border of the groove forms the outer margin of the finger and bears five sharp triangular teeth, excluding the apical tooth, and decreasing in size from the tip backward ; behind these are two blunt teeth. The inner margin bears a single blunt tooth just proximal to the tip, and more proximally still becomes rounded off and no longer sharp. A point of tomentum fills a groove placed between the proximal ends of the outer and inner margins. The immobile finger is similar, with a groove for the tomentum on the outer surface, whose lower border ends in an apical tooth and is continuous with the inner margin of the finger, which bears a single sharp tooth ; the outer margin, which is the upper border of the groove, bears four strong triangular teeth, with two smaller rounded teeth behind them ; a point of tomentum fills a groove between

the proximal portions of the outer and inner margins. In both fingers the outer surface is much broader than the inner, so that the toothed outer margins approximate much more readily than the sharp inner margins; (ix) the peraeiopods are heavy, the length of the propodite being in the proportion of 8 to 5 to its breadth, but they are not nodose as in *D. australiensis*.

The carapace is strongly arched and almost hemispherical, the tomentum is even, interspersed with some few longer hairs; the cervical grooves are the only ones visible, and appear to cross posteriorly forming a small depression at the point of crossing.

The cheliped has an epipodite and the sternal grooves end together on the first walking-leg segment, while the fifth leg is about as long as the third and has a thorn on the outer side of the last joint, i. e., the specimen is a *Dromiopsis* (vide Borradaile, 1903 c, p. 298).

Distribution.—Abrolhos.

Subtribe **BRACHYGNATHA.**

Superfamily *OXYRHYNCHA*.

Family MAMAIDÆ.

3. *EPHIPPIAS ENDEAVOURI* (Rathbun, 1918).

Locality.—1 ♂, Sandy Island, Abrolhos. In a poor state of preservation.

Measurements (in mm.) :—

C. l.	30
C. b.	21
L. of W.-L. 1 ...	l. of dorsal border of moropodite (24)+l. of dorsal border of 3 distal segments (32) = 56.

The chelipeds and walking-legs are not so massive as in Rathbun's type, and the spines are not so definitely sharp nor the tubercles so well defined. The typical saddle-shaped posterior hump is not so prominent, but the specimen has been crushed in this region. A fine specimen, collected off Fremantle, is in the Western Australian Museum.

Distribution.—Abrolhos. Fremantle. Kangaroo Island, S.A. (116); N.S.W. (73).

4. *HUENIA PROTEUS* (de Haan, 1839).

Maia (*Huenia*) *proteus* de Haan, 1839, p. 95, pl. xxii, figs. 4-6.

Huenia proteus Alcock, 1895, p. 195, *ubi synn.*

Locality.—1 ♂, Broome, W.A. (Fisheries Dept.).

Measurements (in mm.) :—

C. l. (without rostrum)	17
R. l.	8 (R. l. - C. l. = 0.47)
C. b. (including spines branchial region)	13
Interorbital b.	5
Ch. l.	26
The eye is 3 mm. behind the preocular spine.	

The walking-legs are lost. A long filamentous seaweed growth arises from the sides of the rostrum just in front of the preocular spine.

The specimen is similar to that of Adams and White, 1848, pl. iv, fig. 4 a. In Laurie's specimens (Laurie, 1906, p. 372) the ratio R. l. \div C. l. varies from 0.36 to 0.45. As in his specimens, the inferior surface of the rostrum is sharp-edged and the tip sharp. Along either side of the upper borders of the rostrum there is a line of closely set, downward curving hairs of a yellowish colour, as in *H. proteus* var. *tenuipes* (Adams and White, 1848, p. 22, pl. iv, fig. 5).

On the gastric region there are three small tubercles arranged in a triangle with the apex pointing posteriorly, as in *Simocarcinus simplex* var. *pyramidatus* (Laurie, 1906, p. 373). In previously published figures and descriptions, and in all the specimens examined in the collection of the British Museum (Natural History), these are represented by a low elevation in the middle line.

The merus joint of the chelipeds has on its dorsal border three little spines in series with equal distances between them. the most distal is well-developed, the two proximal tuberculiform. These were present in all specimens examined. The carpus is almost globiform.

Distribution.—N.W. Australia (114) : N. Australia (46, 84, 23, 104, 119) ; Broome. Hawaii (110) ; S.W. Malay (2) ; India, Ceylon (2) ; Maldives and Laccadives (20) ; Red Sea, Persian Gulf (69) ; Seychelles (113).

5. *MENÆTHIUS MONOCEROS* (Latreille, 1825).

Menæthius monoceros Alcock, 1895, *ubi sup.*

Localities.—a, 2 ♀, Broome, γ F, c, 1 ♀, dredged between Rat Isl and and Pelsart group, Abrolhos ; d, 1 ♂ small, Sandy Island, Abrolhos ; e, 1 ♂, Abrolhos.

Measurements (in mm.) :—

	a.	b.	c.	d.	e
C. l. \div R. l.	20	20	12	10	15
C. l. \div R. l.	4	5	4	3.3	3.75
C. l. \div Ch. l.	1.43	1.43	1.33	1.0	0.83
C. l. \div W.-L. 1 l. .	..	1.11	1.09	1.11	1.07
C. b.	14	13	8	6.5	10
Interocular b. ..	5	5	3.5	2.5	4

Distribution.—Indo-Pacific. Abrolhos. N.W. Australia (84) ; N. Australia (23, 36, 46, 84, 85) ; S.E. Australia (31) ; Fiji, Rotuma (16) ; Hawaii (110) ; N.E. Malay (76, 112) ; S.W. Malay (64, 76) ; Maldives and Laccadives (20) ; Red Sea, Persian Gulf (69) ; East Africa (104) ; Seychelles (113).

6. *PARANAXIA SERPULIFERA* (Guérin-Ménéville, 1834 ?).

Pisa serpulifera Guérin, 1834 ?, pl. viii, fig. 2.

Naxia serpulifera H. Milne-Edwards, 1834, p. 313. Nec *Naxia* (Leach) Latreille, 1825 (*vide* Rathbun, 1897, pp. 163-167), *q.* = *Pisa aurita* (Latreille, 1825) = *Halimus* (*vide* McCulloch, 1913).

Naxia serpulifera Miers, 1879.

Naxioides serpulifera Rathbun, 1897, part. Nec *Naxioides* A. Milne-Edwards, 1865 b.

Paranaxia serpulifera Rathbun, 1924.

Miers, 1879, combines *Naxia* (H. Milne-Edwards, 1834) and *Naxioides*

(A. Milne-Edwards, 1865); Rathbun, 1897, preferred *Naxioides* to *Naxia* (preocc. by (Leach) Latreille, 1825). Genotype of *Naxioides* is *N. hirta* (A. Milne-Edwards, 1865). Rathbun, 1924, separates *Paranaxia serpulifera* as a distinct genus. *Naxia* (Leach) Latreille, 1825, has *Pisa aurita* (Latreille, 1825) as genotype; this is congeneric with *Halimus* (Latreille, 1828) *aries* (Latreille, 1825) the type-species of *Halimus*; *Naxia* therefore replaces *Halimus* (vide McCulloch, 1913, p. 321).

Localities.—*a*, 1 ♀, Geraldton, W.A.; *b*, 1 ♂, Wooded Island, Abrolhos; *c*, 1 ♀, Geraldton, W.A., dried specimen collected by Mr. J. Clark.

Measurements (in mm.):—

	<i>a.</i>	<i>b.</i>	<i>c.</i>
C. l.	127	91	117
C. l. : C. b.	1.27	1.22	1.27
C. l. : R. l.	4.78	4.14	4.87
Interocular b. . .	25	18	23
Ch. l.	94	65	90
W.-L. 1 l.	134	106	131
W.-L. 2 l.	109	75	101

A. Milne-Edwards, 1865 *b*, distinguished his *Naxioides* from *Naxia* (i. e., *Paranaxia*) by a hiatus in the inferior border of the orbit and by the absence of a preocular spine. Miers, 1879, demonstrated the insufficiency of this criterion of separation. Rathbun, 1924, gives other grounds of distinction.

In the orbit of *Naxioides*, in dorsal view, there is a distinct tooth protruding from the upper border of the postocular cup into the supraorbital hiatus. In the specimens in the collection of the British Museum (Natural History) this tooth is sharp-pointed and straight in *N. spinifera* (Borradaile, 1903 *b*), *N. petersii* (Hilgendorf, 1878=*Podopisa* vide Miers, 1879, p. 658), *N. investigatoris* (Alcock, 1895), and *N. hystrix* (Miers, 1886), sharp and curved slightly outward in *N. robillardii* (Miers, 1882), more or less blunt in *N. hirta* (A. Milne-Edwards, 1865 *b*, *q.*=*N. petersii* according to Alcock, 1895), and broad and square in *N. taurus* (Pocock, 1890). Further, in these species there is a distinct spine, either sharp or blunt, on the antero-lateral corner of the basal antennal joint (vide Miers, 1886, p. 59; Alcock, 1895, p. 216). In *N. hirta* this spine is tuberculiform, as noted by A. Milne-Edwards, 1865 *b*, and it is only in this species that it is more than moderately blunted.

In *Paranaxia serpulifera* neither of these spines is represented. Specimens were examined from the collection of the British Museum (Natural History) ranging from 1.9 cm. to 12.7 cm. in carapace length. Rathbun's figures, also, of post-larval forms (Rathbun, 1914, p. 611, pl. ii, figs. 9, 10) show them not to be present.

Further, the basal antennal joint is expanded laterally at its base as a broad blunt prominence nearly completely filling the floor of the orbit, leaving a very small hiatus between it and the postocular cup. In *Naxioides*, there may be a spine, a spiniform tubercle (*N. hirta*), or a slightly rounded prominence (*N. robillardii*) in this position. Again, the hiatus in the supraorbital border is wide in all the species of *Naxioides*; in *Paranaxia serpulifera* it is present

only in the very youngest specimens. It is a "triangular sinus" in Rathbun's newly hatched specimens, a narrow cleft in the specimen of carapace length 1.9 cm., a still narrower cleft in those of 2.0 cm. and 2.2 cm., and is closed entirely in that of 3.7 cm. In the full-grown adult there is nothing but a closed groove to mark the hiatus.

The position of the antennal flagellum differs in the two genera. In *Naxioides* it is plainly visible in dorsal view on one side or other of the rostral spines; only in *N. robillardii* is there any difficulty in seeing it thus, and in it the flagellum can usually be distinguished to the inner side of the spines. In *Paranaxia*, except in the very smallest specimens, not a trace of the flagellum is visible in dorsal view past the rostral spines.

The rostral spines themselves in *Naxioides* are long, tapering, and of varying degrees of divergence, the least divergent being in *N. hirta*. There is an accessory spinule, which is small, never more than one-quarter the length of the part of the rostral spine which projects beyond it, and is always developed on the medial side of the spine; whether it is developmentally the original tip of the spine is not known. In *Paranaxia serpulifera* the rostral spines are about a quarter as broad as long, are straight and parallel, and bifid into two subequal spines at the tip. Rathbun, 1914, has shown that the medial develops first as the true tip of the spine and that the lateral develops as the accessory spinule.

The chelipeds and ambulatory legs in *Paranaxia* are stout, and the dactyli markedly curved; in *Naxioides* the chelipeds and legs are "slender and moderately developed" and the dactyli "nearly straight" (Alcock, 1895).

Hyastenus (White, 1847 b) is distinguished from *Naxioides* by the absence of the accessory spinule on the spines of the rostrum. As doubt has been expressed of the validity of this distinction, it is noteworthy that in *Hyastenus* the tooth standing in the supraorbital hiatus, described above in *Naxioides*, is either absent or represented by a small tubercle, never by a sharp spine; whereas the spine at the antero-lateral angle of the basal antennal joint is prominent, though it may be either sharp or blunt.

Alcock's description of the subfamily Pisinae (Alcock, 1895, p. 216), "eyes with commencing orbits of which one of the most characteristic parts is a large blunt, usually but not always cupped postocular process into which the eye is retractile, but never to such an extent as to completely conceal the cornea from dorsal—still less from ventral—view," does not apply to *Paranaxia serpulifera*, the cornea being completely hidden from dorsal view when retracted.

Distribution.—Abrolhos; Geraldton; Monte Bello Islands (114); C. Jaubert (119); Shark Bay (84); N. Australia (23; 46).

7. CYCLAX (CYCLOMAIA) SUBORBICULARIS (Stimpson, 1858).

Cyclax (Cyclomaia) suborbicularis Alcock, 1895, p. 245, *ubi synn.*

Cyclax suborbicularis Laurie, 1915, p. 410

Localities.—a-k, 9 ♂, 1 ♀, 1 ♀ ovig., Long Island, Abrolhos; l, 1 ♀ ovig., Pelsart Island; m-n, 2 ♂, Wooded Island.

Specimen *g* is parasitised by a Rhizocephalan and is beginning to take on a female form of abdomen.

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>	<i>d.</i>	<i>e.</i>	<i>f.</i>	<i>g.</i>	<i>h.</i>
C. l.	36	30	30	26	24	14	21	26
C. l. ÷ C. b.	1	1	1.03	1	.96	1.17	1	.96
C. l. ÷ Interorbital b.	2.57	2.31	2.31	2.17	2.18	2.33	2.1	2.36
C. l. ÷ Ch. l.60	1.0	.66	1.0	..	1.04
C. l. ÷ W.-L. 1 l.80	.81	.8277	..	.86
	<i>i.</i>	<i>j.</i>	<i>k.</i>	<i>l.</i>	<i>m.</i>	<i>n.</i>	<i>x.</i>	
C. l.	27	12	11	23	20	18	40	
C. l. ÷ C. b.97	1.09	1.2	1.15	1.11	1.12	1.03	
C. l. ÷ Interorbital b.	2.45	2.0	2.0	2.3	2.2	2.1	2.66	
C. l. ÷ Ch. l.	1.0	.95	1.0	1.25	
C. l. ÷ W.-L. 1 l.82	.74	.82	.83	

The measurements under *x* are taken from Rathbun's figure (Rathbun, 1893, pl. viii, fig. 2).

The chelipeds in *a* and *c* are far larger than in the other specimens, and are swollen and glabrous ; a similar variation occurs in *Schizophrys dama* (Herbst, 1804) in old males (*vide* Alcock, 1895, p. 244). The spines are less acute throughout, and the carapace more hairy than in Rathbun's figure (*l. c.*). A small spine in the medial part of the lower border of the orbit is very conspicuous and pointed in some of the specimens, being in this respect unlike specimens in the British Museum (Natural History).

Distribution.—Abrolhos. N. Australia (23). Fiji (16). S.W. Malaya (2) ; India, Ceylon (2) ; Red Sea (69) ; E. Africa, Seychelles (113).


8. SCHIZOPHRYS DAMA (Herbst, 1804).

Schizophrys aspera Alcock, 1895, p. 343, *ubi synn.*

Cancer dama Herbst, 1804, p. 5, pl. lxx, fig. 5.

Schizophrys dama Alcock, 1895, p. 245, *et synn. et auct.*

Mithrax aspera H. Milne-Edwards, 1832.

Localities.—*a*, 1 ♂, Wooded Island, Abrolhos ; *b-e*, 4 ♂, Broome,  ; *f*, 1 ♀, Coral-flats, East Wallaby Island.

In addition to the specimens in the collection, a series of 15 specimens of *S. aspera* and 1 of *S. dama* from the Collection of the British Museum (Natural History) was examined. They are indicated on p. 421 by the numbers 1 to 16.

Measurements (in mm.).

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	a.	b.	f.	c.	d.	16.	e.
	♀.	♂.	♂.	♀.	♀.	♂.	♂.	♂.	♂.	♂.	♀.	♂.	♂.	♂.	♂.	♂.	♂.	♀.	♂.	♂.	♂.	♂.
C.L.	27	32	27	20	13	37	12	12	12	12	16	30	19	18	25	14	12	20	31	23	35	34
C.b.	24	28	23	17	11	31	10	10	10	10	13	24	15	14	19	10.5	9	15	22.5	17	26	25
C.L÷C.b.	1.12	1.14	1.17	1.18	1.18	1.19	1.20	1.20	1.20	1.20	1.20	1.23	1.25	1.27	1.29	1.32	1.33	1.33	1.35	1.35	1.35	1.36
R.L.	4	5	4	3	2	7	2	2	2	2	2	5	2.5	2	4	2	17	3	6	4	8	5
C.L÷R.L.	6.75	6.4	6.75	6.6	6.5	5.3	6.0	6.0	6.0	6.0	8.0	6.0	7.6	9.0	6.25	7.0	7.0	6.75	5.15	5.75	4.4	6.8
2nd Accessory rostral spinule.	0	0	0	0	0	Trace.	0	0	0	0	0	0	0	0	0	Very small.	Trace right, 0 left.	0	Sharp, right, Tubercle, left.	0	Distinct.	Small right.
Subhepatic spine.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	Very small.	Tuberculiform.	Tubercles.	Tubercles.	Tubercles.	Tubercles.	Tubercles.


The differentiation of *S. aspera* (Milne-Edwards) and *S. dama* (Herbst) appears not to be justified. *S. aspera* has been distinguished by (i) the less elongate form of the carapace, (ii) the shorter rostrum, (iii) one accessory spinule on the rostral horn (instead of two in *S. dama*), (iv) the ventral spine on the subhepatic region, and (v) the uneven and sharply tubercular granulation of the carapace (*vide* Alcock, 1895, p. 245). As can be seen, a series can be made in which the ratios C. l. \div C. b. and C. l. \div R. l. range from 1.12 to 1.36 and 4.4 to 9.0 respectively. Alcock (*l. c.*) gives the typical ratio C. l. \div C. b. as 1.11 in *S. aspera*, 1.33 in *S. dama*. In *a* there is no second accessory rostral spine, but there is a very small subhepatic spine with another of almost equal size close to it; in *b* there is a trace of the second rostral spinule on one side, but none on the other, and the subhepatic tooth is represented by an inconspicuous tubercle; in *c* there is a sharp second accessory rostral spinule on the right, and a tubercle on the left, and in *e* the spine is very small on the right side. In *c*, *d*, *e*, and *f* the subhepatic spine is represented by a series of tubercles.

16, *c*, and 6 have relatively the longest rostra, and there is a trace of a second accessory spinule in the latter, which, however, has a relatively broad carapace and a well-developed subhepatic spine. The granulations of the carapace differ very little in the series, even when examined under a lens. *c*, which has the longest carapace, has a relatively short rostrum. The variations are not correlated with sex, as the table on p. 421 shows. The size of the chelipeds, however, varies considerably, these being slender in the females and small males, but large and heavy in the better-grown males. There is some evidence that the "facultative dimorphism" noted by Geoffrey Smith (Smith, 1906, p. 312) occurs in *S. dama*; 6 in the above series, though the largest male, has small slender chelipeds; in 12 the chelæ are much longer, but still slender; but 2 and 3, though not fully grown, have much heavier and stouter chelipeds.

In the figure of A. Milne-Edwards, 1872 (pl. x, figs. 1, 1 *a-c*), the rostrum is shown as having three spines on each horn—a terminal one, a lateral one, and a medial dorsal one. None of the specimens examined exhibit this character; and in those which come in the *S. dama* end of the series the extra rostral spine is posterior to and in series with the terminal and lateral spines.

The distribution would seem to indicate that the forms inhabiting more temperate seas tend to fall into the *S. dama* end of the table, those in more tropical seas into the *S. aspera* end.

Distribution.—Abrolhos; N.W. Australia (84, 119); S.W. Australia (84); S.E. Australia (116); N. Australia (23, 46, 84, 116, 119); N.E. Malay (103, 76); S.W. Malay (64, 65, 77); Christmas Island (24); India, Ceylon (2); Red Sea, Persian Gulf (69); Seychelles (113); S. Africa (124).

9. *MICIPPA PHILYRA* (Herbst, 1803).*Micippa philyra* Alcock, 1895, p. 249 *ubi synn.**Localities*.—*a-b*, 1 ♂, 1 ♀, Broome, ; *c*, 1 ♀ ovig., Long Island, Abrolhos.*Measurements* (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>
C. l.	41	35	19
C. b.	33	27	15
C. l. C. b.	1.24	1.29	1.26
Deflexed portion of rostrum to point of bifurcation....	15	14	5
Antenna 1	12	—	—
2nd segment of antenna 1 ..	4.5	—	2
Hand l.	17	12	7
Hand b.	5	3	2.5
Rostrum b. at origin	14	—	6

The spines on the lateral borders are not conspicuously knobbed.

Distribution.—Abrolhos ; N.W. Australia (84) ; N. Australia (23, 46, 84) ; N.E. Malay (112) . S.W. Malay (64, 65) ; India, Ceylon (2) ; Red Sea, Persian Gulf (69) ; E. Africa (104).10. *NAXIA AURITA* (Latreille, 1825).*Pisa aurita* Latreille, 1825, p. 140.*Halimus auritus* Milne-Edwards, 1834, p. 341.*Halimus loricis* Haswell, 1880, p. 435, Baker, 1905, p. 119, pl. xxi, figs. 1 1 a ; McCulloch, 1908, p. 54.*Naxia aurita* McCulloch, 1913, p. 327.*Locality*.—1 ♀ ovig., Abrolhos Islands.*Measurements* (in mm.) :—

C. l.	46
C. l. = C. b.	46 34—1.35
C. l. l. Rostral horn	46 6—7.66
C. l. l. Interorbital b.	46 12—3.83
C. l. Ch. l.	46 41—1.12
C. l. W.-L. l. l.	46 53 0.868

Distribution.—Abrolhos ; S.W. Australia (46, 72) ; S.E. Australia (46, 10, 71).

Family HYMENOSOMIDÆ.

Genus HALICARCINUS (White, 1846).

Halicarcinus Kemp, 1917, p. 243.11. *HALICARCINUS AUSTRALIS* (Haswell, 1882). (Pl. 27. figs. 4, 4 a.)*Hymenosoma australe* Haswell, 1882 c, p. 115, pl. iii, fig. 2.*Hymenicus australe* Tesch, 1918 a, pp. 7, 13.*Halicarcinus australe* Montgomery, 1921, p. 93.*Localities*.—*a-e*, ♂, Swan River, Perth, W.A. ; *g-h*, 1 ♂, 1 ♀, on weed at Boat-sheds, Swan River.

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>	<i>d.</i>	<i>e.</i>	<i>g.</i>	<i>h.</i>
C. l. (without rostrum) . . .	16	15	15	14	12.5	13.5	11.5
C. b.	18	18	17.5	17	14.5	16	14
Front. orb. b.	6	6	5.5	5.5	4.5	5	4.5
Rostrum b. (at base) . . .	3	3	2.5	2.5	2	2.5	2
Rostrum l.	3	3	3	3	2.5	2.5	2

Tesch retains in the family Hymenosomatidæ the genera *Hymenosoma* (Desmarest, 1825), *Halicarcinus* (White, 1846), *Hymenicus* (Dana, 1851 *b*), *Trigonoplax* (H. Milne-Edwards, 1853), *Elamena* (H. Milne-Edwards, 1837), *Elamenopsis* (A. Milne-Edwards, 1873 *b*), and *Rhynchoplax* (Stimpson, 1859). Kemp, while disagreeing with Haswell that *Hymenosoma*, *Halicarcinus*, and *Hymenicus* are synonyms, unites the two latter, with reservations, under *Halicarcinus*; many species formerly placed under *Hymenicus* he refers, with reserve, to *Rhynchoplax* (Stimpson).

Tesch refers to *Hymenosoma* two species—the genotype *H. orbiculare* (Desmarest, 1825) and *H. depressum* (Jacquinot & Lucas, 1853); the latter, as shown by specimens in the Natural History Museum, South Kensington, has a distinct epistome, so that Kemp is correct in regarding *H. orbiculare* as the sole species of the genus. The position of *H. depressum* is doubtful, but it is certainly not a *Hymenosoma*.

Kemp is correct in considering the shape of the rostrum as an insufficient criterion for the separation of *Halicarcinus* and *Hymenicus*. A series of variations can be made out which serve to connect *Hymenicus varius*, Dana's genotype (Dana, 1851 *b*, p. 290) with *Halicarcinus planatus*, the genotype of White (White, 1846, p. 178). A series can be made of *H. planatus*, *H. varius*, *H. australis*, and *H. rostratus* (Haswell, 1882 *b*), the spines of the rostrum becoming progressively more completely fused at the base and the middle spine growing longer. Following Kemp, I designate this species *Halicarcinus australis*; under Tesch's arrangement, it would be *Hymenicus*.

Haswell's figure is remarkably accurate, as far as it goes. The rostrum is deflexed and concave from side to side, and with three teeth which vary in development from being almost absent to being sharp and prominent; the middle tooth is on a lower plane than the other two, and is slightly more developed. The "two obscure teeth" on the sides of the carapace also vary, being absent in one case, and never more than a rudiment. The external maxillipedes completely close the buccal cavern, conforming to Kemp's description of the genus, and the sutures of the male abdomen are distinct.

The epistome is strong and wide.

The chelipeds in three cases are very broad and deep and carry a pulvinus between them which is much better developed than Haswell shows in his figure. In other cases the claws are not so deep, nor so sharp and thin along

the inferior border ; but the pulvinus is still present. Possibly this is another case of facultative dimorphism.

Distribution.---Swan River ; S.E. Australia (35, 46).

12. *HALICARCINUS BEDFORDI*, sp. n. (Pl. 27. figs. 3, 3 a, 3 b.)

Hymenosoma sp. Montgomery, 1921, p. 95.

Locality.---a c, 3 ♂ ovig., dredged, Swan River, The Narrows.

Measurements (in mm.) :—

	a.	b.	c.
C. l.	5	4	4.5
C. b.	4.5	4	4

There is a well defined epistome, the regions of the carapace are well defined, the merus and ischium of the external maxillipedes, which completely fill the buccal cavern, are of about equal length, and the rostrum is triangular.

The upper surface of the carapace, excluding the rostrum, is roughly circular, being just under 5 mm. long and about 4.5 mm. broad : it is smooth and hairless and the regions are reasonably well marked : there is a slight ridge completely encircling this upper surface and cutting it off from the rostrum.

The rostrum is triangular, projects straight out in the plane of the upper surface of the carapace, and covers the antennules and antennæ, which fold beneath it, from dorsal view. The rostrum ends in a blunt point and is slightly concave upwards : it is slightly sinuous at its edges and near its base are two very small tubercles which are situated over the eye-stalks, and correspond to the two lateral teeth of *H. australis*. The edges of the rostrum are fringed with short curved hairs.

The side-walls of the carapace are nearly vertical in front, but further back become progressively nearer the horizontal : this brings the insertions of the walking-legs clearly into a dorsal view, the last leg, in fact, being inserted almost on a level with the upper surface of the carapace.

The antennules fold beneath the rostrum, so as to be hidden from above, and are separated at their base by a septum which thins off anteriorly so that the two antennæ come to lie side by side.

The eyes are set beneath the rostrum and are carried on fairly long stalks. They project forward, reaching about three-quarters of the way to the tip of the rostrum.

The external maxillipedes completely close the buccal cavern. The ischium and merus together form nearly a rectangle and they are separated by a line drawn from the end of the third fifth on the medial side to the end of the second fifth on the outer side. The antero-external angle of the ischium is slightly sinuous and curled over ; and at the antero-internal angle is carried the small flagellum. The exognath is between a quarter and a third as broad as the merus, and is clearly seen throughout the greater part of its length. It bears a flagellum.

The chelipeds are slender, barely stouter than the legs ; the palm and wrist

are slightly turgid, the former being a little longer than the fingers. The merus is somewhat bowed and about twice as long as the carpus. The fingers are not toothed.

The walking-legs are slender, and the third pair are about three times the length of the carapace. Both chelipeds and walking-legs have some scattered hairs on their surface. The dactyli are sharp, strongly curved at the tip, about two-thirds the length of the propodite, and bear on their curved edge a fringe of curled hairs.

Distribution.—Swan River.

13. *ELAMENA TRUNCATA* (Stimpson, 1858). (Pl. 27. fig. 21.)

Elamena truncata Alcock, 1900 a, p. 386.

Elamena truncata Baker, 1906, p. 112, pl. ii, fig. 2.

Elamena truncata Tesch, 1918 a, p. 22, pl. i, fig. 4. *ubi synn.*

Locality.—1 ♂, Sandy Island, Abrolhos.

Measurements (in mm.) :—

C. l.	7.5
C. b.	7.5
W.-L. 1 l.	15.5

This specimen agrees with Baker's (Baker, *l. c.*) in having the carapace as long as broad, and with some of his specimens in having the carapace slightly concave, not depressed : both Kemp (1917, fig. 22) and Tesch (1918 a, pl. i, fig. 4) figure the species as broader than long, so that it is possible that there is a distinct Australian species. In the figures of Tesch and Baker there are slight variations to be noted with regard to the eyes, antennæ, and external maxillipedes. The postocular tooth, which Alcock states to be absent and Baker omits from his figure, is present in the Abrolhos specimen. There is no "very prominent, waved, sharp rim" on the pterygostomian region as Tesch describes, but there is a "conical obliquely compressed tubercle" of large dimensions as mentioned by Baker. Possibly Tesch's "three lobes" are the very slightly prominent external angle of the orbit, this compressed tooth, and another, obliquely behind it but smaller, at the base of the first walking-leg.

The epistome is stated by Tesch to be "short but distinct, deeply sunk," by Baker to be "well-developed and not depressed." In the Abrolhos specimen it is well-defined, not depressed, and bears on its lower border a pair of laminated plates projecting perpendicularly, and separated by a notch in the centre ; these plates overhang the buccal cavern like an eave, and the external maxillipedes fit in beneath them, closing the buccal cavern completely, with the exognath almost entirely visible. Baker's description and figure of the external maxillipede are closer to this specimen than those of Tesch.

The male abdomen differs from Tesch's specimens in that the penultimate segment, while shorter than the preceding one and the terminal one, is not shorter than both the preceding segments. As Kemp states, guided by Baker's

figures, segments 3 and 4 are fused and 5 is free ; there is an indication of a line of fusion to be seen is shown in the figure.

Distribution.—Abrolhos ; S.E. Australia (11) ; Fiji, Rotuma (16) ; S.W. Malay (7) ; India, Ceylon (7).

Superfamily *BRACHYRHYNCHA*.

Family PORTUNIDÆ.

14. *PORTUNUS PELAGICUS* (Linnaeus, 1758).

Neptunus pelagicus Alcock, 1899 *a*, p. 34, *ubi synn.*

Lupa pelagicus Stebbing, 1908, p. 11 ; 1910, p. 307.

Portunus pelagicus Rathbun, 1897, pp. 155, 160.

Localities.—*a*, 1 ♂, Wallaby Island, Abrolhos ; *b-c*, 4 ♂, Wooded Island, Abrolhos.

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>	<i>d.</i>	<i>e.</i>
C. l.	44	32	29	29	22
C. b. to tips of spines	97	72	66	64	46
l. lower border of left palm ...	—	40	34	35	24
b. left palm	—	9	8	8	6
l. 6th abdominal tergum	11	8	7	7	5
Ant. b. 6th abdom. tergum ...	12	11	10	8	7
Post. b. 6th abdom. tergum ..	8	6	4	5	3

This is the common edible crab of the Swan River, where the size attained is much greater than in the Abrolhos specimens. The colour varies from slaty-blue to dull brown.

Specimen *a* has the chelipeds in course of regeneration. They appear as a bud enclosed in a single cuticular sac, through which the position of the joints between the meropodite, carpopodite and propodite, and the mobile finger are discernible as grooves. The costæ of the arm and hand appear as low ridges.

In *b* there are 8 teeth on the right antero-lateral border, and the normal 9 on the left. One doubts the value of these teeth as diagnostic characters.

Distribution.—Abrolhos. Swan River. Indo-Pacific. N.W. Australia (84) ; S.W. Australia (84) ; S.E. Australia (46, 31, 134) ; N. Australia (23, 36, 84, 118) ; N. Zealand (80) ; Funafuti (135) ; N.E. Malay (65, 76, 112) ; S.W. Malay (5, 64, 76, 77) ; India, Ceylon (5) ; Red Sea, Persian Gulf, (5, 69) ; S. Africa (124).

15. *THALAMITA PRYMNA* (Herbst, 1803) var. *PELSARTI*, var. n. (Pl. 24. fig. 2 ; Pl. 28. figs. 3, 3 *a*.)

Localities.—*a*, 1 ♂, dredged inside lagoon, Pelsart Island ; *b*, 1 ♂, Long Island, Abrolhos.

b has in its chela the broken-off claw of another crab, probably *Cyclax* (*Cyclomaia*) *suborbicularis* Stimpson.

Measurements (in mm.) :—

	a.	b.
C. l.....	35	22
C. b.	55	33
Lower border left palm l.	41	23
" " b.....	13	6
6th abdom. tergum l.	6	4
6th abdom. tergum b.	6	4

The carapace is about two-thirds as long as broad as in var. *crenata* (Milne-Edwards, 1834) * ; there is a dense short tomentum and the transverse ridges are very distinct—*cf.* var. *dancæ* (Stimpson, 1859) and var. *annectans* (Laurie, 1906) ; the mid-gastric ridge is continued following the line of the orbits to the interval between the first and second antero-lateral teeth, unlike var. *prymna* Herbst, 1803) †. The front has the two most lateral teeth smaller than the rest, which are closely set, the two middle ones projecting slightly and on a lower level, recalling var. *prymna* ; the supraorbital lobes are fairly broad. The dorsal aspect of the carapace reminds one perhaps more of the *T. admete* (Herbst, 1803) group than of any of those with an eight-lobed front. The fourth tooth of the antero-lateral borders is small, but not rudimentary as in var. *stimpsoni* (A. Milne-Edwards, 1861) and var. *annectans*. The basal antennal joint is very broad, being about three-eighths the carapace breadth ; as in var. *prymna* it bears a row of spines. The chelipeds are most like those of var. *dancæ* in this group : they are (i) slightly unequal ; (ii) covered with granules on all surfaces, except the costæ of the fingers and part of the under surface of the arm ; (iii) have four teeth on the upper surface of the arm, the fourth being terminal and on a lower plane than the other three, which increase progressively in size as one passes distally ; (iv) have on the posterior border of the arm a series of squamiform granules, with an imbricated appearance ; (v) have four large teeth on the wrist, that at the inner angle being very strongly marked, and three costæ, each marked by a row of granules ; (vi) have six spines in two rows on the upper border of the hand ; (vii) have two marked costæ on the outer border of the hand running towards the upper and lower borders of the immobile finger ; these costæ are cut into numerous closely set over-lapping blunt teeth ; (viii) have the whole of the lower and inner surface of the hand covered with slightly imbricating squamiform granules ; these are largest at the junction of the inner and lower surfaces and on the costate ridge in the middle of the inner surface. The greater part of the chela

* = *Thalamita crenata* (Latr.) Edw. Alcock, 1899 a, p. 76. Milne-Edwards, not Latreille, must be regarded as the author of the species, as Latreille did not publish the name ; it is, according to Milne-Edwards, that of a specimen in the Paris Museum. *Vide* Opinion 1 of International Commission on Zoological Nomenclature (Proc. Biol. Soc., Washington, xxxix, 1926, p. 91).

† The typical variety of Herbst is designated var. *prymna* on the analogy of typical subgenera bearing the name of the genus—*vide* Art. 10 International Rules of Zool. Nomenclature (l. c. p. 77).

is clothed with a fine tomentum, through which the spines and granules appear. The fingers are costate and ringed near the tip with a dark band. In characters (i) and (iv) this variety resembles var. *danae*, in (vi) and (vii) is like var. *annectans*; but the chelipeds really are most like those of the allied *T. admete* group with a two-lobed front.

The propodite of the last pair of legs is serrated throughout the length of the posterior border (cf. var. *prymna*).

Distribution.—Abrolhos, W.A.

15 a. THALAMITA PRYMNA (Herbst, 1803) var. PROXIMA, var. n. (Pl. 24. fig. 1; Pl. 29. figs. 1, 1 a.)

Localities.—a-b, 2 ♂, North Island, Abrolhos.

Measurements (in mm.) :—

	a	b.
C. l.	50	36
C. b.	77	56
Lower border left palm l.	53	42
Left palm b.	16	14
6th abdom. tergum l.	8	6
6th abdom. tergum posterior b.	9	7

In general appearance, these are very similar to var. *pelsarti*, but differ in the same way that var. *stimpsoni* differs from var. *prymna*—namely, that the ridge on the basal antennal joint is granular rather than toothed. The ridges on the carapace are similar, but the larger specimen *a* has little tomentum, being smooth and glabrous, except just anterior to the ridges. In the front, the two middle teeth are slightly overlapped by the two next lateral to them; in var. *pelsarti* the overlapping is not marked, though the middle teeth are on a lower plane. In a ventral view, there is a strong smooth ridge running down from the lower aspect of the lateral frontal tooth towards the epistome, separating the antennular fossa from the inner end of the basal antennal joint. The chelipeds differ from those of var. *pelsarti* in the following characters :— (ii) the granules are not so general and are absent from the lower surface of the hand; (iii) there are three teeth only on the upper surface of the arm, the fourth being represented by a blunt prominence; (iv) the posterior border of the arm has no granules, but is ridged in a manner recalling “ ripple-marking ”; (vi) there are only five spines on the upper border of the hand, the most proximal of the median row being absent; (vii) the granules on the costae of the palm are blunt, not tooth-like; (viii) the lower surface of the hand is smooth—a band of granules, representing a ridge in var. *danae*, separates it from the inner surface.

Distribution.—Abrolhos, W.A.

The two varieties support the view of Kossmann, 1877, adopted by Alcock, 1899 a, p. 76, Calman, 1900, p. 22, and Laurie, 1906, p. 419, that all the *Thalamitas* with an eight-lobed front are specifically identical. These two bear more


resemblance to one another than they do to any other member of the group, but they have affinities with var. *danæ* and var. *stimpsoni* (whose close relationship has been noted by de Man, 1888 *a*, p. 78), and with var. *prymna*, var. *crenata*, and var. *annectans*; the carapace and chelipeds, moreover, approach very closely to those of some of the two-lobed front *T. admete* group, especially *T. margaritimana* (Rathbun, 1911, p. 208, pl. i, fig. 12) and *T. granosimana* (Borradaile, 1902 *a*, p. 202).

The varieties of *T. prymna*, therefore, include these two, *T. prymna* (Herbst, 1803), *T. crenata* (Milne-Edwards, 1834), *T. danæ* (Stimpson, 1859), *T. stimpsoni* (A. Milne-Edwards, 1861), *T. picta* (Stimpson, 1859) (for all of which vide Alcock, 1899 *a*), and *T. prymna* var. *annectans* (Laurie, 1906). In addition, there are three varieties described by Calman, 1900, p. 22. The following artificial key, modified from Alcock, may serve to separate the varieties:—

- Extreme breadth of basal antennal joint far greater than major orbital diameter; front cut into eight lobes, including the broad inner supraorbital lobes.
- Submedian lobes of front half as broad again as median lobes = Calman c.
- Submedian lobes not much broader than, equal to, or less than median lobes 1.
1. Ridge on basal antennal joint:—
- (a) with tooth-like, smooth entire edge = var. *picta*.
- (b) with a row of granules 2.
- (c) with a row of teeth 6.
2. Five teeth in antero-lateral border, 4th equal to or larger than 5th = var. *crenata*.
- 4th tooth of antero-lateral border smaller than 5th 3.
3. Three medial pairs of frontal lobes ill-separated, only marked off by indistinct notches = Calman b.
- Three medial pairs of frontal lobes distinctly marked off from one another 4.
4. A ridge, either of granules or entire, separating inner from inferior surface of hand 5.
- No ridge separating these surfaces = var. *stimpsoni*.
5. Ridge, separating these surfaces, composed of granules = var. *proxima*.
- Ridge, separating these surfaces, faint and entire = var. *danæ*.
6. 4th tooth of antero-lateral border rudimentary or absent 7.
- 4th tooth of antero-lateral border not so complete a rudiment 8.
7. Transverse ridge on gastric region continued to notch between 1st and 2nd antero-lateral teeth = var. *prymna*.
- Transverse ridge not so continued = var. *annectans*.
8. Hand granular over all surfaces = var. *pelsarti*.
- Hand not granular over all surfaces Calman a.

16. *THALAMITA SIMA* (Milne-Edwards, 1834). (Pl. 29. fig. 2.)

Thalamita sima, Alcock, 1899 *a*, p. 81, *ubi synn.*

Localities.—a, 1 ♂, dredged off Wallaby Island, Abrolhos; b, 1 ♂, North-West Australia. 

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>
C. l.	27	24.5
C. b.	4.5	37
Frontal lobe b.	7.5	7
Supraorbital lobe b.	5.5	4.5

The supraorbital lobes are exactly intermediate between those of the *T. admete* and *T. chaptalii* groups, being slightly arched and about three-fourths the width of one of the frontal lobes; in *T. chaptalii* (Audouin, 1826) the proportion is two-thirds or less, in *T. admete* (Herbst, 1803) and *T. integra* (Dana, 1852 *a*) about five-sixths; in the former the supraorbital lobe is distinctly arched, in the latter nearly straight.

The chelipeds are approximately equal; the "transverse squamiform granules" of Alcock's description (Alcock, 1899 *a*, p. 81) on the lower surface of the hand are very characteristic, being in two longitudinal series, giving an appearance exactly like maize in a cob. The movable finger bears a black band not far from the tip.

Distribution.—Abrolhos: N.W. Australia (84); S.W. Australia (84); S.E. Australia (46, 84, 85, 134); N. Australia (23, 36, 46, 84, 85, 104, 119, 127); N. Zealand, N. Caledonia (80, 84); Hawaii (110); N.E. Malay (112); S.W. Malay (77); Red Sea, Persian Gulf (5, 69).

17. *THALAMITA MACROPUS*, sp. n. (Pl. 24. fig. 4; Pl. 28. figs. 2, 2 *a.*)

Locality.—1 ♀, East Wallaby Island.

Measurements (in mm.) :—

C. l.	11
C. b.	17
Posterior border of C.	5

This species stands between *T. investigatoris* (Alcock, 1899 *a*) and *T. exetastica* (Alcock, 1899 *a*). The median lobes of the front are on a lower level than the others, as in *T. exetastica*, but are much narrower than the submedian as in *T. investigatoris*. The front is like *T. exetastica* var. *macrodonta* (Borradaile, 1902 *a*, p. 203), but it is distinguished by having the fifth tooth of the antero-lateral border the largest and the fourth at least as large as any of the rest; no mention is made of a large fourth tooth in any of the described species, though references to a large fifth tooth are common (*vide* Laurie, 1906, p. 420; Rathbun, 1911, p. 209).

Alcock's description of *T. exetastica* reads "4th and 5th being extremely small" (Alcock, 1899 *a*, p. 86); but his figure (Alcock, 1900 *b*, pl. xlvii, fig. 2) shows them as of moderate size. *T. macropus* bears at the base of the first antero-lateral tooth a small accessory spinule as in *T. exetastica*.

The chelipeds are like those of *T. investigatoris* with regard to the granulations, but the spines, which are strong and sharp, are disposed exactly as in *T. sima*;

the fingers, as in *T. exetastica*, are as long as the palm. The legs are very long and slender, and the propodite of the last leg is smooth, without spines.

The general form of the carapace is more like that of *T. investigatoris* than of *T. exetastica*, being about two-thirds as long as broad and with the posterior border less than two-fifths the breadth.

It seems probable that Borradaile is correct in considering *T. investigatoris*, *T. exetastica* and its varieties, and *T. imparimanus* (Alcock, 1899 *a*) as but varieties of yet another highly variable *Thalamita* (*vide* Borradaile, 1902 *a*, p. 204).

Distribution.—Abrolhos, W.A.

18. *THALAMITA DAKINI*, sp. n. (Pl. 24. fig. 3 ; Pl. 28. fig. 4.)

Locality.—1 ♂, Wooded Island, Abrolhos.

Measurements (in mm.) :—

C. l.	11
C. b.	18
Posterior border of C. b.	6
Basal antennal joint b.	3.5
Major diam. of orbit	2.5
Middle frontal lobe b.	2.5

This species further complicates the problem of the genus *Thalamita*. The striking features are the basal antennal joint and the front. As is shown above, the extreme extent of the basal antennal joint is neither " far greater than the major diameter of the orbit " nor is it " equal to or less " (Alcock, 1899 *a*, p. 73). The proportion between the breadth of the basal antennal joint and the carapace breadth is 2 : 9 in *T. prymna* var. *crenata*, 1 : 4 in *T. prymna* and *T. admete*, 1 : 5 or 6 in *T. chaptalii* ; and in *T. investigatoris* it is less than, in *T. imparimanus* less than half, and in *T. sexlobata* about equal to the major diameter of the orbit. *T. dakini* agrees, therefore, in this respect most nearly with *T. chaptalii*.

There is a ridge of granules on the basal antennal joint. The orbits have a slight dorsal inclination as in *T. sexlobata* (Miers, 1886) and *T. oculatea* (Alcock, 1899 *a*).

The front is four-lobed, excluding the inner supraorbital lobe, but the two lateral lobes are very small and are minutely toothed at their margins ; from these a line of granules continues on in the line of the front beneath the inner supraorbital lobe, between it and the extension into the orbit of the basal antennal joint. The front is thus unique among the *Thalamitas*.

The inner supraorbital lobes are slightly concave forwards, and each is about equal in extent to the middle frontal lobes, though disposed on an alignment behind and above these ; the front is slightly flexed downward. The carapace is hairy and the lines of the carapace are disposed much as in *T. admete*. The teeth of the antero-lateral border are five in number, the fourth being small. The posterior border of the carapace is straight and about one-third the greatest breadth of the carapace.

The chelipeds are smooth on the inner and lower borders, spined, granular, costate, and hairy on the upper and outer surface. The spines are disposed as in *T. sima* with the addition of an extra large spine on the upper border of the hand; the spines are everywhere sharper and the granules tend to be spiny.

The hands bear three costae on the outer surface, which are granular, the granules tending to be sharp. The fingers are stumpy, but strongly denticulated.

The legs are stout and costate; the propodite of the last pair of legs is hairy, but not spined.

Distribution.—Abrolhos, W.A.

Family CANCRIDÆ.

Subfamily THINÆ.

19. *KRAUSSIA HENDERSONI* (Rathbun, 1902).

Kraussia nitida Alcock, 1899 *a*, p. 98. *Nec* Stimpson, 1859, p. 40.

Kraussia hendersoni Rathbun, 1902, p. 132; Balss, 1922, p. 97.

Locality.—1 ♂, Wooded Island, Abrolhos.

Measurements (in mm.) :—

C. l.	11
C. b.	13
Frontal-orbital b.	6.5
Last joint of W.-L. 2 l.	3.7
Last joint of W.-L. 2 b.	1.2

The specimen supports Rathbun's differentiation of *K. nitida* (Stimpson) and *K. hendersoni* at all points, including the sharp granules on the inner angle of the wrist, and the denticulations on the last three joints of the walking-legs, points which differ from the description of *K. nitida* by Alcock (*l. c.*), whose specimens are taken by Rathbun to be *K. hendersoni*. Henderson's figure exaggerates the grooves running back from the inner angle of the orbit and also the prominence of the front (*vide* Henderson, 1893, pl. xxxvii, fig. 9).

The fingers of the chelipeds are much less stumpy than in *K. nitida*, the movable finger being about as long as the greatest breadth of the palm.

Distribution.—Abrolhos; Hawaii (110); S.W. Malay (5); India, Ceylon (5); Japan (14); Maldives (109).

Family XANTHIDÆ.

20. *LIOMERA CINCTIMANA* (White, 1847 *a*).

Liomera cinctimana Alcock, 1898, p. 88, *ubi synn.*

Carpilodes cinctimana Odhner, 1925, p. 9.

Localities.—*a-d*, 1 ♀ ovig., 3 ♂, Long Island, Abrolhos; *e*, 1 ♀, Abrolhos.

Measurements (in mm.) :—

	a.	b.	c.	d.	e.
C. l.....	19	14	12	12	21.5
C. b.	36	26	22.5	22	40
Fronto-orbital b.	12	10	8.5	9	14
Post. border of C. b.	10	7.5	6	6	13

The specimens show considerable variation in colour, and in all the characteristic dark band on the hand is absent or incomplete. The colour varies from pink to red and orange-red, and in *c* the fingers and tips of the dactyli are light brown : in *e* this lightening of the colour is patchy, so that the coxopodites of the chelipeds and the pterygostomian region in their vicinity are a porcelain white, and there are patches of white on the other legs ; there is a white band separating the black claw at the end of the dactylus from the orange-red at the base.

The big ♂ *e* has on the chelipeds a very distinct groove on the outside of the hand running down towards the movable finger ; this is only faintly marked in the other specimens. The lobulation of the antero-lateral borders is also much more deep than in the others.

I follow Odhner (Odhner, 1925, p. 9) and Stimpson (Stimpson, 1907, p. 38) in considering *Liomera* congeneric with *Carpilodes* in part ; the character of the basal antennal joint is quite a variable one and cannot be used as of generic importance. Odhner, however, though pointing out that *Liomera* has precedence over *Carpilodes* (Dana, 1851 *a*, pp. 124, 126), retains *Carpilodes* as the generic name—a procedure entirely unjustifiable.

Distribution.—Abrolhos. N. Australia (23, 36) ; S.W. Malay (4) ; Maldives and Laccadives (18) ; Red Sea, Persian Gulf, (4, 69) ; E. Africa, Seychelles (4, 113).

21. *LIOMERA BELLA* (Dana, 1852).

Carpilodes rugatus Alcock, 1898, p. 85. *Nec* A. Milne-Edwards, 1865 *a*, p. 230.

Carpilodes bella Odhner 1925, p. 16, pl. i, fig. 9.

Localities.—*a-c*, 2 ♀, 1 ♂, Long Island, Abrolhos ; *d-e*, 1 ♀, 1 ♂, Wooded Island, Abrolhos ; *f*, 1 ♂, Sandy Island, Abrolhos.

Measurements (in mm.) :—

	a.	b.	c.	d.	e.	f.
C. l.....	9	8	8	9	8	8.5
C. b.	16	14	14	17	14.5	15
Fronto-orbital b.	7.5	7	7	8	7	7.5
Posterior border of C. b. ...	5.5	4.5	4.5	5.5	5	5

The variations in colour in this species are through white (*a*), pink and white (*d*), to pink (*f*) and purple. In (*d*) the anterior portion of the carapace is pink, but it is white posteriorly and underneath, and on the major portion of the legs. The chelipeds show a variation in colour similar to that in *L. cinctimana* ; in (*d*) the light brown coloration of the tips of the dactyli extends along the

whole of the underside of the palm; in (*f*) it is distinctly¹ visible in this situation, but does not extend the whole distance. In (*f*) the lower border of the palm is remarkable for a distinct smooth area, in a position which is well granulated in all the others. In the purple specimens, the tips of the dactyli and the fingers of the chelipeds are white instead of brown at the tip and shade off into purple through a light brown.

Distribution.—Abrolhos : N. Australia (46) ; Fiji, Rotuma (35) : Hawaii (110) : N.E. Malay (76) ; S.W. Malay (4, 76) ; Christmas Island (24) ; India, Ceylon (4) ; Maldives and Laccadives (18) ; Red Sea, Persian Gulf (4, 69) ; Seychelles, E. Africa (4, 113). *Vide* also Odhner, 1925. Not in S. Africa, *vide* Stebbing, 1910.

22. *LOPHOZOZYMUS PULCHELLUS* (A. Milne-Edwards, 1867).

Lophozozymus pulchellus A. Milne-Edwards, 1867, p. 273; 1873 *a*, p. 205, pl. vi, fig. 3; Rathbun, 1911, p. 214.

Locality.—1 ♂, Wooded Island, shore.

Measurements (in mm.) :—

C. l.	15
C. b.	25
Fronto-orbital b. ...	11.5
Post. border of C. b.	8

Distribution.—Abrolhos ; India, Ceylon (68) ; Red Sea, Persian Gulf (69) ; Seychelles, E. Africa (113).

23. *XANTHO IMPRESSUS* (Lamarck, 1818).

Xantho impressus Alcock, 1898, p. 115, *ubi synn.* ; Odhner, 1925, p. 79.

Localities.—*a*, 1 ♂, Wooded Island, Abrolhos ; *b-c*, 2 ♀, Wooded Island, Abrolhos ; *d*, 1 ♀ ovig., Long Island ; *e*, 1 ♀ ovig., Abrolhos.

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>	<i>d.</i>	<i>e.</i>
C. l.	25	30	25	30	29
C. b.	43	52.5	42.5	50	51.5

Distribution.—Abrolhos ; S.W. Malay (4, 77) ; E. Africa, Seychelles (4, 113). *Vide* also Ortmann, 1894 *a*, pp. 444, 449.

24. *XANTHO HYDROPHILUS* (Herbst, 1790).

Cancer hydrophilus Herbst, 1790, i, pt. 8, p. 266, pl. xxi, fig. 124.

Xantho affinis de Haan, 1835, p. 48, pl. xiii, fig. 8.

Chlorodius exaratus Milne-Edwards, 1834, i, p. 402.

Xantho (Leptodius) exaratus Alcock, 1898, p. 118.

Leptodius exaratus Rathbun in Stimpson, 1907, p. 52, pl. vi, figs. 3-4, 6-9.

Xantho hydrophilus Stebbing, 1908, p. 7, *ubi synn.* ; 1910, p. 297 ; Laurie, 1915, p. 444.

Localities.—*a-b*, 2 ♂, Reefs, North Island, Abrolhos ; *c-o*, 4 large ♂ ; 9 small immature specimens, West Wallaby Island, Abrolhos ; *p-q*, 1 ♂, 1 ♀ ovig., between Pigeon Island and Wallaby Island, Abrolhos.

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>	<i>d.</i>	<i>e.</i>	<i>f.</i>	<i>g.</i>	<i>h.</i>	<i>i.</i>
C. l.	16.5	14.5	14	12	11.5	11.5	7.5	7	6.5
C. b.	26.5	22.5	22.5	18.5	18	18	11	11	10
Fronto-orb. b.	13.5	12	11.5	10	10	10.5	7	6.5	6
Post. border of C. b. .	10	8	8	6.5	6.5	6.5	4	4	3.5

	<i>j.</i>	<i>k.</i>	<i>l.</i>	<i>m.</i>	<i>n.</i>	<i>o.</i>	<i>p.</i>	<i>q.</i>
C. l.	6	6	5	4.5	3.5	2.5	11	9
C. b.	9	8.5	7.5	7	5	4	17	14
Fronto-orb. b.	6	6	5	4.5	4	3	9.5	8
Post. border of C. b. .	3	3	2.5	2.5	2	1.5	6.5	5

Along with specimens *p* and *q* there is a large piece of sponge which fits on obviously to the carapace as a commensal cap such as is carried by some Dromiids. From which specimen it comes is uncertain ; possibly it was from the female, which might explain the great preponderance of males in the collection.

The specimens approximate most closely to Stimpson's variety "*h*," *latus*. They differ from the typical specimens in having the antero-lateral teeth trimmed with a series of subsidiary teeth, and in having the sculpturing of the carapace less marked—for example, on the gastric region, in the typical specimen, there is a longitudinal groove dividing the region and a transverse one medial to it on either side ; these are absent in the Abrolhos specimens. The outer angle of the orbit is on a slightly higher level than that of the antero-lateral borders.

Distribution.—Abrolhos ; N.W. Australia (84) ; S.E. Australia (46) ; N. Australia (23, 36, 46, 84) ; Funafuti (135) ; Hawaii (110) ; N.E. Malay (112) ; S.W. Malay (4) ; Christmas Island (24) ; India, Ceylon (4) ; Maldives and Laccadives (4, 18) ; Red Sea, Persian Gulf (4, 65) ; Seychelles (113). *Vide* also Ortmann, 1894 *a*, p. 445.

25. *ACTÆA HELLERI* (A. Milne-Edwards, 1865 *a*).

Actæa helleri Odhner, 1925, p. 77, fig. 7, *ubi synn.*

Nec *Actæa helleri* de Man, 1888 *b*, p. 261; *q.* = *A. depressa* (White, 1847 *b*), *vide* Odhner, 1925.

Locality.—1 ♂, Long Island, Abrolhos.

Measurements (in mm.) :—

C. l.	38
C. b.	57

The lobulation of this species is like that of *A. depressa* (White, 1847 b), but it is readily distinguished by the much greater breadth of the carapace.

The specimen is much larger than those formerly described, comparing with Nobili's largest, 29 mm. broad (Nobili, 1906, p. 256), and Rathbun's, 15.3 mm. broad (Rathbun, 1911, p. 221, pl. xviii). The species is quite like *A. hirsutissima* (Rüppell, 1830, p. 26, pl. v, fig. 6), from which it can be distinguished by the following points.

The under surface of the carapace is minutely granular, not hairy, and there are no grooves or fissures subdividing the antero-lateral borders. There are no bristles on the external surface of the maxillipedes or on the distal abdominal terga; nor are there hairs on the sternum or proximal abdominal terga. The lobulation of the carapace is not so distinct, the hairs are much more sparse posteriorly and are yellowish instead of black. The antero-lateral borders are scarcely lobulated.

The hand of the chelipeds is short and stumpy, exactly as in Odhner's figure (Odhner, 1925, p. 78, fig. 7), except that the hairs are sparser and not so long. In *A. hirsutissima* the hand is long, narrow, and costate.

Distribution.—Abrolhos; N. Australia (100); N.E. Malay (87); Red Sea, Persian Gulf (69); Seychelles (113); S. Africa (125).

26. *ACTEA CALCULOSA* (Milne-Edwards, 1834).

Actea calculosa Alcock, 1898, p. 152, *ubi synn.*

Actea calculosa Calman, 1900, p. 8

Locality.—1 ♂ with *Sacculina*. Dredged between Wallaby and Pelsart Islands.

Measurements (in mm.) :—

C. l.	10
C. b.	14
Fronto-orb. b.	8
Posterior border of C. b.	5

The basal antennal joint just reaches the orbit, but the specimen is fully adult. The fingers of the chelipeds are black, not brown, and the teeth on the fingers are not very marked.

It is noteworthy that not only this specimen but also two out of four of the following species are parasitised by a *Sacculina*, whereas only one out of twenty specimens of *A. depressa* (White, 1847) var. *abrolhensis* in the collection is so infected.

Distribution.—Abrolhos; N.W. Australia (84, 100); S.W. Australia (84, 100); S.E. Australia (84, 100, 118); N. Australia (23, 36, 46, 84, 100, 119); N.E. Malay (112); S.W. Malay (4); India, Ceylon (4); Red Sea, Persian Gulf (4, 69).

27. *ACTÆA SAVIGNYI* (Milne-Edwards, 1834).

Actæa granulata Alcock, 1898, p. 151, *et synn.*; Calman, 1900, p. 8.

Nec *Cancer granulatus* Fabricius, *vide* Kossman, 1877, p. 25.


Nec *Cancer granulatus* Linnaeus, 1758, *vide* Rathbun, 1910, p. 350.

Actæa savignyi Kossmann, 1877, *et* Rathbun, 1910, *l. c.*

Actæa granulata Laurie, 1915, pp. 414, 447.

Actæa savignyi pura Balss, 1922, p. 122.

Actæa savignyi Odhner, 1925, p. 52.

Locality.—*a-d*, 1 ♂ with *Sacculina*, 1 ♀ with *Sacculina*; 2 ♀, Broome, .

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>	<i>d.</i>
C. l.	14	14	28.5	14.5
C. b.	17.5	17.5	21.5	18
Fronto-orbital b.	10.5	10.5	15	10.5
Post. border of C. b.	6	6	10	6

The specimens are relatively large when compared with the majority hitherto described.

Distribution.—N.W. Australia (100); S.E. Australia (46, 134); Broome; N. Australia (46, 85, 119); N. Zealand (80); N.E. Malay (112); S.W. Malay (4); India, Ceylon (4); Maldives and Laccadives (18); Red Sea, Persian Gulf (4, 69); Seychelles (113).

28. *ACTÆA DEPRESSA* * (White, 1847 *b*) var. *abrolhensis*, var. n.

Localities.—*a-f*, 2 ♂, 4 ♀, Long Island; *g*, 1 ♂, North Island; *h* n, 5 ♂, 2 ♀ (one with *Sacculina*), Wooded Island; *o-q*, 1 ♂, 2 ♀, Sandy Island; *r-s*, 2 ♂, Abrolhos; *t*, 1 ♂, inside lagoon, Pelsart Island.

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>	<i>d.</i>	<i>e.</i>	<i>f.</i>	<i>g.</i>	<i>h.</i>	<i>i.</i>	<i>j.</i>
C. l.	16	14.5	12.5	10	10	8.5	20.5	20.5	15	9.5
C. b.	21.5	20	17	14	14.5	11	28	28	21	13.5

	<i>k.</i>	<i>l.</i>	<i>m.</i>	<i>n.</i>	<i>o.</i>	<i>p.</i>	<i>q.</i>	<i>r.</i>	<i>s.</i>	<i>t.</i>
C. l.	8	7	13.5	12	16.5	13.5	8	17	12.5	8.5
C. b.	11	9	19.5	17	22.5	18	10.5	23	17.5	11

These specimens are not quite like those described by Odhner, but approach *A. depressa* (White, 1847 *b*) more closely than any other species. The granules of the carapace are fewer, coarser, and sharper than in Odhner's specimens,

* *Actæa depressa* (White) = *Actæa parvula* Alcock, 1898, p. 146. Nec *Menippe parvula* de Haan, 1833, *nom. nud.* Vide Odhner, 1925, p. 38, pl. ii, fig. 19, *ubi synn.*

some of which have been compared from the collection of the British Museum, Natural History. The grooves of the carapace are deeper and the granules are unevenly scattered; there is some variation among the individual specimens, but generally the granulation is more marked over the posterior two-thirds of the carapace than typically. The fur is variable in amount, but is often so long as to mask the areolæ: in all cases it is longer than typically.

The lobulation of the antero-lateral border of the carapace also varies in the collection, and in one specimen (s) the border is entire.

The chelipeds also show variation. In some cases the pigmentation is confined to the fingers, in others it covers the whole lower border of the hand and part of both its inner and outer surfaces. The chelipeds are stumpy, the palm is not quite so broad at the base of the immobile finger as shown in Odhner's figure (Odhner, *l. c.* pl. iii, fig. 13 *a*), and the two big teeth are not so prominent; in none is the cheliped so long and narrow as in *A. parrula* (de Haan, 1833) [*vide* Odhner, *l. c.* pl. ii, fig. 19].

Distribution.—Abrolhos, and *vide* Odhner, *l. c.*

29. *ACTÆA RUFOPUNCTATA* (Milne-Edwards, 1834).

Actæa rufopunctata Alcock, 1898, p. 142, *ubi synn.*

Actæa garretti Rathbun, 1906, p. 852, pl. ix, fig. 8.

Actæa rufopunctata var. *retusa* Nobili, 1905, p. 404.

Localities.—*a*, 1 ♂, Long Island, Abrolhos: *b*, 1 ♂, Wooded Island, shore-collecting.

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>
C. l.	10	9
C. b.	15.5	14
Fronto-orbital b.	8.5	7.5
Post. border of C. b.	5	4.5

The red colouration on certain of the lobules is beautifully preserved; the whole of the lobule is not coloured, but only the anterior two-thirds or three-quarters.

Distribution.—Abrolhos; Fiji, Rotuma (16); Hawaii (110); S.W. Malay (4, 76, 77); N.W. Malay (100); Christmas Island (24); India, Ceylon (4); Maldives and Laccadives (18); Red Sea, Persian Gulf (69); E. Africa (104); West Indies (100).

30. *ACTÆA LEVIDORSALIS*, sp. n. (Pl. 26. figs. 3, 3 *a*, 3 *b*, 3 *c*.)

Locality.—1 ♂, Long Island, Abrolhos.

Measurements (in mm.) :—

C. l.	14
C. b.	22
Fronto-orbital b.	11
Front b.	7

The carapace is about two-thirds as long as broad, arched fore and aft, almost flat transversely across the branchial regions. The areolation of the carapace is very incomplete, being almost absent over the posterior part of the gastric and branchial regions, and over the intestinal region; the granulation is microscopic in these areas. Anteriorly, areolæ are well marked and covered with conical granules which are in no case squamiform. There is very little hair on the carapace, not more than fifty or sixty hairs being present all told; there is a row of about eight in a groove behind the front, about five on either side in a groove on the branchial region, and a little tuft of six to eight at the junction of the gastric and branchial regions on either side; a few appear between the lobules of the front.

The front is deflexed, divided by a well-marked median fissure, there being on each side a broad median lobe and a small lateral lobe, which is fairly sharp and separated by a groove from the outer orbital angle. The orbit shows a small indentation above and below the outer orbital angle, which is ill-marked; in the lower border of the orbit, the inner angle forms a pronounced forwardly projecting tooth. The antero-lateral borders show four lobes, excluding the external orbital angle; the first three bear teeth, the first of which is obsolescent, the second larger, and the third fairly well marked; the teeth bear secondary spiny granulations.

The chelipeds are about equal and are granular over the whole outer surface. Three costæ, granular throughout, appear on the outer surface of the hand, the upper one being broad low, and looking as if it were double. Hairs are very sparse, and there is no prominent spine, except for a blunt double tooth at the antero-internal angle of the carpus. The colour of the fingers is bluish black, lightening to brown at the tips; the colouration does not extend along the lower border of the palm. The walking-legs have a line of conical granules, almost dentiform, along the upper margin of the femur, which is otherwise smooth; the more distal joints are granular, particularly on the outer aspect, and are sparsely hairy above and below.

The lack of lobulation and granulation posteriorly suggest *Lioxantho* (Alcock, 1898): there is also a superficial resemblance to *Xantho* (particularly the *Leptodius* species) in the anterior part. The front, however, is that of an *Actæa*, though one expects a greater degree of sculpture and areolation. *A. hawaiiensis* (Rathbun, 1906, p. 853, pl. ix, fig. 9) appears to approach this species closely, but is distinguished by:—(i) the carapace is "narrow" (not, however, in Rathbun's figure); (ii) the regions are deeply separated and granules scaly; (iii) the hairs on the carapace are more numerous; (iv) the walking-legs and chelæ are more hairy; (v) the colour of the fingers runs far on to the palm; (vi) the orbits have two V's above and one below the outer orbital angle; (vii) the last antero-lateral tooth is narrow, simple, and almost upturned.

Distribution.—Abrolhos.

31. *PARAXANTHIAS ELEGANS* (Stimpson, 1859).

Xanthodes elegans Stimpson, 1859, p. 33.

Xanthias elegans Rathbun, in footnote to Stimpson, 1907, p. 47, pl. v, fig. 3, and 1897, p. 165.

Xanthodes atromanus Haswell, 1882 a.

Xanthodes atromanus Grant & McCulloch, 1906, p. 12.

Paraxanthias elegans Odhner, 1925, p. 84.

Localities.—*a*, 1 ♂, Wooded Island ; *b*, 1 ♀, Long Island ; *c*, 1 ♀, between Pigeon Island and Wallaby Group.

Measurements (in mm.) :—

	<i>a</i> .	<i>b</i> .	<i>c</i> .
C. l.	10	10.5	4.5
C. b.	15	15	7
Fronto-orbital b.	9	9.5	5
Post. border of C. b.	5.5	5.5	3

The areolations of the carapace are not quite so distinct as in specimens preserved in the British Museum (Natural History), which came from the Australian Museum. The triangular tooth on the inner angle of the lower orbital margin is distinct, as described by Haswell, but this tooth is indicated in *Xanthias notatus* (Dana, 1852) also.

The specimens agree well with the description and figures of Stimpson (Stimpson, 1907, p. 47, pl. v, fig. 3), except that the hands are much more tuberculated. The granulations on the outer side of the palm are more numerous than in the types of *Xanthodes atromanus* (Haswell) ; there are four rows of granules below the groove on the upper part of the palm instead of two ; in the British Museum specimens these two extra rows are indicated but not well developed. The fingers vary considerably : in the British Museum specimens, in some the fixed finger is as long as the depth of the palm, in others only half this. Grant and McCulloch (*l. c.* p. 12) draw attention to the variability of colour in this species, " deep chocolate mottled to almost white," the specimens from 17 fathoms being much lighter than " those from the reef " ; the fingers are described as black, the black extending " far down the palm." In the Abrolhos specimens and in many of the British Museum specimens the black does not extend far along the underside of the palm, and its extent is very variable.

Distribution.—Abrolhos : Japan (127) ; N.W. Australia (114) ; S.E. Australia (31, 46, 134) ; N. Australia (36) ; Norfolk Island (37).

32. *CHLORODIELLA NIGRA* (Förskal, 1775).

Chlorodius niger Alcock, 1898, p. 160, *et synn.* ; Balss, 1921, p. 62 ; Odhner, 1925, p. 85.

Chlorodiella nigra Rathbun, 1897, p. 165 ; Balss, 1922, p. 130 ; Laurie, 1915, p. 447 *et synn.*

Localities.—*a-b*, 2 ♂, shore-collecting, Long Island ; *c*, 1 ♀, shore-collecting, north end of Pelsart Island ; *d*, 1 ♂, Wooded Island.

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>	<i>d.</i>
C. l.	16	13	15.5	11
C. b.	24	20.5	23	18
Fronto-orbital b.	18	16	18	14
Front b.	12.5	11	12	10
Left Ch. l.	44	38	38	32

As in Laurie's Ceylon specimens (Laurie, 1906, p. 405), *a* and *b* have the last two antero-lateral teeth blunt, not "terminating in procurved spine-like points" (Alcock, *l. c.*); there is a tendency to a forward curve, however, plainly visible even in the blunt teeth. In *c* the last tooth is a procurved spine, in *d* the last two as Alcock describes. The anterior border of the arm is tuberculate in *b* and *c*, spined in *d*, but merely slightly sinuous at its middle in *a*. The carapace under a lens is minutely pitted in appearance.

For the variability of this species *vide* Laurie, 1915, p. 447.

Distribution.—Abrolhos : S.E. Australia (31, 46, 84) ; N. Australia (23, 36, 46, 84, 118) ; Fiji, Rotuma (16) ; Hawaii (110) ; N.E. Malay (65, 76, 112) ; S.W. Malay (4, 64, 76, 77) ; Christmas Island (24) ; India, Ceylon (4) ; Maldives and Laccadives (18) ; Red Sea, Persian Gulf (69) ; E. Africa (104, 113).

33. *PHYMODIUS UNGULATUS* (H. Milne-Edwards, 1834).

Phymodius unguatus Alcock, 1898, p. 162, *ubi synn.*

Phymodius monticulosus Alcock, 1898, p. 163, *ubi synn.*

Chlorodius monticulosus Dana, 1852, p. 79.

Chlorodius obscurus Lucas, 1852, p. 26, pl. iii, fig. 4.

Phymodius obscurus Rathbun, 1906, p. 858 ; Rathbun, 1907, p. 46.

Phymodius unguatus Nobili, 1906 ; Rathbun, 1906, p. 857 ; Laurie, 1915, p. 450, *ubi synn.*

Localities.—*a-d*, 4 ♂, shore, Long Island, Abrolhos ; *e*, 1 ♀, shore, Long Island, Abrolhos ; *f-h*, 2 ♂, 1 ♀, dredged, Long Island, Abrolhos.

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>	<i>d.</i>	<i>e.</i>	<i>f.</i>	<i>g.</i>	<i>h.</i>
C. l.	22	18.5	15.5	13.5	12	17.5	17	17
C. b.	32.5	26	22	19	16.5	26.5	25	24.5
Fronto-orb. b.	20	17	14.5	13	11	16	15.5	15.5
Post. border of C. b. .	10	8	7	6	5	7.5	9	8.5

Distribution.—Abrolhos ; S.E. Australia (31) ; N. Australia (23, 36, 46) ; Fiji, Funafuti (16, 135) ; Hawaii (110) ; N.E. Malay (104) ; S.W. Malay (4) ; Christmas Island (24) ; India, Ceylon (4, 68) ; Maldives and Laccadives (18) ; Red Sea (69) ; Seychelles (113) ; E. Africa (104) ; S. Africa (124).

34. CHLORODOPSIS AREOLATA (Milne-Edwards, 1834).

Chlorodius areolata Milne-Edwards, 1834, p. 400.

Chlorodopsis areolata Alcock, 1898, p. 166, *et synn.*

Etisodes cælatus Dana, 1852, p. 118, pl. ix, 1855, fig. 4.

Actæodes affinis Dana, 1852, p. 197, pl. xi, 1855, fig. 5.

Actæa affinis A. Milne-Edwards, 1865 *a*, p. 263.

Actæodes affinis Miers, 1886, p. 135. *Nec A. tomentosus.*

Actæa affinis Rathbun, 1906, p. 852; 1907, p. 42; 1911, p. 219; 1914, p. 658; Borradaile, 1900, p. 583; 1902 *b*, p. 255. *Nec* Lanchester, 1900, p. 734 *q.* = *A. hirsutissima* (Rüppell).

Chlorodopsis areolata Rathbun, 1906, p. 858; Bouvier, 1915, p. 101; Odhner, 1925, p. 36.

Localities.—*a-j*, 4 ♂, 3 ♀, 3 ♀ ovig., Wooded Island, Abrolhos; *k-m*, 3 ♂, Long Island; *n*, 1 ♀ ovig., Abrolhos; *o*, 1 ♀, Swan River.

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>	<i>d.</i>	<i>e.</i>	<i>f.</i>	<i>g.</i>	<i>h.</i>
C. l.	19.5	16.5	14	15	13.5	14	11.5	15
C. b.	26	23	21	22	18	19	17	21
Fronto-orbital b.	17	14	13	15	11	12	10.5	13.5
Front b.	11	10	9	10	8.5	9	8	9.5

	<i>i.</i>	<i>j.</i>	<i>k.</i>	<i>l.</i>	<i>m.</i>	<i>n.</i>	<i>o.</i>
C. l.	15	13	15	13	12	14.5	8.5
C. b.	22	19	22	20	18	21.5	12
Fronto-orbital b.	14	12	14	12	11	13	8
Front b.	9.5	8	10	9	8	9.5	5.5

k has two legs in course of regeneration. The buds come out in a single envelope, which is, however, marked with indentations where the individual joints are to occur.

A very constant character in these specimens is a pair of lobules over the intestinal region, placed like a pair of outstretched wings, which have fewer granules and less dark hair than the rest, making them appear lighter in colour. The only figure of *Actæodes affinis* (Dana) illustrates these areolets.

Alcock, 1898, p. 166, describes the fingers as "smooth except for some grooving and granulations at the base of the dactylus." There are two rows of granules on the upper border of the movable finger: these granules enclose a gutter between them which is continued almost to the tip of the finger, beyond the point to which the granules reach.

The subspinous granules on the walking-legs described by Alcock as "peeping through" the fur, are only conspicuous in the male specimens.

Distribution.—Abrolhos; Swan River; N.W. Australia (114); S.E. Australia
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(46, 134); N. Australia (36, 46, 136); Hawaii (110); Palmyra and Fanning Islands (30); S.W. Malay (4); Christmas Island (24); India, Ceylon (4); Maldives and Laccadives (18); Red Sea, Persian Gulf (69); E. Africa, Seychelles (4); S. Africa (124, 125).

35. OZIUS TRUNCATUS (Milne-Edwards, 1834).

Ozius truncatus Grant & McCulloch, 1906, p. 153.

Localities.—*a*, 1 ♀, North Island, Abrolhos; *b*, 1 ♂, island at entrance to lagoon, Wallaby Group.

Measurements (in mm.) :—

	<i>a</i> .	<i>b</i> .
C. l.	28	22.5
C. b.	41	33
Fronto-orb. b.	22	17.5
Post. border of C. b.	9.5	8.5

Distribution.—Abrolhos; S.E. Australia (31); N. Australia (36, 46); N. Zealand, Norfolk Island (37, 46, 80).

36. PILUMNUS CONTRARIUS (Rathbun, 1923).

Locality.—1 ♂, Swan River.

Measurements (in mm.) :—

C. l.	7
C. b.	9.5
Front b.	3.5
Front. orb. border	5.5
W.-L. 1 l.	4.5 + 4 + 3 = 11.5
W.-L. 2 l.	4.5 + 4 + 3 = 11.5
W.-L. 3 l.	4.5 + 4 + 3 = 11.5
W.-L. 4 l.	4 + 3.5 + 2.5 = 10
W.-L. 1 b. of femur.	1

This specimen is referred to Miss Rathbun's species with considerable reserve.

The carapace is curved, but not strongly, both fore and aft and transversely, is about three-quarters as long as broad, with a smooth surface, covered all over with a rather thin covering of long soft hairs; between these is a shorter fur which is also fairly sparse. The regions are visible, but there is no definite areolation. The front is deflexed and divided by a shallow groove into two lobes, which are little prominent, and which run almost in continuity with the supraorbital border, only a rudiment of a lateral lobe being present. In the supraorbital border are two very ill-marked emarginations, another being present below the obscure outer orbital angle. The lower border of the orbit ends in a poorly developed tooth at its inner end, and is fringed with hairs. The antero-lateral borders bear four lobes, the first obscure and continuous with the outer orbital angle, the next more marked, and the third and fourth forming blunt teeth, bearing tufts of hairs.

The right cheliped is slightly the larger ; both are smooth externally except for a few low granules above and proximally, the largest being the more distal ; the greater part of the outer surface is covered rather sparsely with hairs and more thickly with fur. The carpus bears a strong tooth at the antero-internal angle. The colour of the fingers is brown, and differs little from the rather muddy colour of the rest of the chela, and, indeed, of the carapace as a whole. The walking-legs are slender, the first three almost of equal length, the last shorter ; the terminal joint is especially elongated and slender.

Distribution.—Swan River ; North Australia (118).

37. PILUMNUS DIGITALIS (Rathbun, 1923).

Locality.—1 ♀ juv., dredged between Rat Group and Pelsart Island.

Measurements (in mm.) :—

C. l.	5.5
C. b.	7.5
Fronto-orb. b.	15.5
Front b.	3.5
Major palm l.	5
„ „ b.	2.5

Distribution.—Abrolhos ; Queensland (118).

38. PILUMNUS EDAMENSIS (de Man, 1888 b) (Pl. 27. figs. 1, 1 a.)

Localities.—a g, 7 ♂, Long Island ; h-r, 13 ♀, Long Island ; u-x, 4 ♀ ovig., Long Island ; y-z, α, 3 ♂, Wooded Island ; β, 1 ♀, Wooded Island ; γ, 1 ♂, inside lagoon, Pelsart group ; δ, ε, 2 ♂, Abrolhos.

Measurements (in mm.) :—

	a.	b.	c.	d.	e.	f.	g.	h.	i.	j.
C. l.	14	14	14	13.5	11.5	8	6	12	12	12
C. b.	19	19	19	18	16	11	8.5	16.5	16.5	16
Fronto-orbital b.	11	11	11	10.5	9	7	5.5	9.5	9.5	9.5
Post. border of C. b. .	7	7	7	6.5	5.5	4	3	5.5	5.5	5.5

	k.	l.	m.	n.	o.	p.	q.	r.	u.	v.
C. l.	11.5	11	11	10	10	10	10	8.5	13.5	12.5
C. b.	16	15	14.5	14	14	14	14	13	18	17
Fronto-orbital b.	9.5	9	9	8.5	8.5	8.5	8.5	8	11	10
Post. border of C. b. .	5.5	5.5	5.5	5	5	5	5	4.5	7	6

	w.	x.	y.	z.	α.	β.	γ.	δ.	ε.
C. l.	12.5	10.5	9.5	9.5	6.5	11	6	14	9
C. b.	17.5	14.5	13	13	9	15	8	19	11.5
Fronto-orbital b.	10	8.5	8	7	6	9	5.5	11	7.5
Post. border of C. b. .	6	5.5	5	5	3.5	6.5	3	7	4.5

There is very little hesitation in placing these specimens in de Man's species ; but the genus *Pilumnus* is having further strain on its already wide boundaries.

Firstly, the division of the Xanthida by the character of the ridges of the endostome breaks down here : the ridges are very poorly developed in the anterior part and are only visible under a powerful lens. The teeth of the antero-lateral border, which one expects to be present in a *Pilumnus*, are scarcely apparent, being almost microscopic and barely more than tubercles. Again, the carapace is almost completely devoid of hair on the dorsal surface, an almost unique occurrence in a *Pilumnus*. The most remarkable feature of the specimens, when fresh, was a ridge of stiff outstanding fulvous hairs about 2 to 4 mm. in length, projecting forward from the antero-lateral borders and the front ; these are visible in the preserved specimens, but are much crushed and broken.

There is considerable variation in carapace colour, from white to light brown, and in the colour of the fingers, from light brown (almost white) to dark brown (almost black).

The antennules are remarkable in that the inner ramus is short, stiff, curved, and pointed, and the outer ramus plumose and curved toward the inner, giving a pseudo-chelate appearance.

The right claw is the smaller and is covered on the outer aspect of the palm with a short fur. The left hand has fur only in about one-sixth of the extent at the base of the outer aspect.

Distribution.—Abrolhos ; N.E. Malay (112) ; S.E. Malay (76).

39. *PILUMNUS PULCHER* (Miers, 1884). (Pl. 25. fig. 2.)

Locality.—1 ♂, Broome (Fisheries dept.).


Measurements (in mm.) :—

C. l.	23
C. b.	30
Front b.	8.5
Fronto-orb. b.	15.5

Distribution.—Broome ; Northern Australia (23, 84, 85, 104, 118, 119).

40. *PILUMNUS SEMILANATUS* (Miers, 1884).

Pilumnus semilanatus Rathbun, 1923, p. 14, pl. xxiv, figs. 1-2.

Localities.—c-e, 1 ♂, 2 ♀, Broome, .

	c.	d.	e.
C. l.	36	25	23.5
C. b.	42	33	29
Fronto-orbital b.	22	18	17
Post. border of C. b.	15	12	11

These specimens agree in every respect except size with those of Miers (Miers, 1884, pp. 183, 222, pl. xxii, fig. B) and McCulloch (McCulloch, 1913, p. 325, fig. 43). The largest measures 46 mm. across the carapace as against

McCulloch's largest, 18 mm. across. The frontal lobes are distinctly notched, as Miers shows in his figure, though not mentioning it in the text. There are two little tufts of hair on the carapace just behind the cardiac region; the granules on the wrist are conspicuous; the fingers are black. These points are given in amplification of Miers's description. The brilliant red colour of the granules on the chelipeds makes the species instantly conspicuous.


Distribution.—Abrolhos; N. Australia (36, 72, 118, 119).

41. *PILUMNUS SPINICARPUS* (Grant & McCulloch, 1906).

Pilumnus spinicarpus Grant & McCulloch, 1906, p. 15, pl. 1, figs. 2, 2 a.

Pilumnus spinicarpus Rathbun, 1923, p. 123.

Pilumnus cursor Alcock, 1898, p. 195. Ntc A. Milne-Edwards, 1873 a, p. 244.

Localities.—1 ♀, Broome, .

Measurements (in mm.) :—

C. l.	8.5
C. b.	12.0
Fronto-orbital b.	8.0
Front b.	4.0
3rd leg l.	19.0

Distribution.—Broome; N. Australia (23, 36, 46, 84, 118); N.E. Malay (76); Andamans (4).

42. *PILUMNUS GRANTI*, sp. n. (Pl. 26. figs. 1, 1 a.)

Locality.—a b, 1 ♂, 1 ♀ ovig., dredged off Long Island.

Measurements (in mm.) :—


	a.	b.
C. l.	16	15
C. b.	20.5	20
W.-L. 1 l.	31	26
W.-L. 2 l.	27.5	26
W.-L. 3 l.	26.5	27
W.-L. 4 l.	22.5	23
Major palm l.	17	13.5
Major palm b.	11	8
Fronto-orb. b.	14	13.5
Front b.	7.5	7

This is a species very near to *P. contrarius* (Rathbun, 1923); in both the tubercles on the major palm increase instead of decreasing in size towards the distal and lower portion. It is distinguished by the following :—(i) the median lobes of the front are much more prominent and sharply rounded, while the outer lobes are obsolete, though slightly acute, and almost coincident with the rounded inner angle of the orbit, from which it is separated by only a slight furrow; (ii) the lateral notch of the front is of the same size as the median, not larger; (iii) the notch in the superior orbital margin is small but distinct and near the outer orbital angle; it is of nearly the same size as the shallow

notch below the outer angle ; (iv) the antero-lateral teeth are four in number, are prominent, and made up of a base covered with accessory low denticles ; the first (or external angle of the orbit) is not low, and but slightly smaller than the second ; the third and fourth are largest and are equal in size. All are much sharper than in *P. contrarius*, where the second is the largest ; (iv) the chelipeds have the lower margins of the arm smooth, not tuberculate, and the inner margin minutely granular only ; the proximal half of the lower margin in the major palm, which is the right, is smooth.

Distribution.—Abrolhos.

43. *PILUMNUS MACCULLOCHI*, sp. n. (Pl. 26. figs. 2, 2 a.)

Locality.—1 ♀, Broome, .

Measurements (in mm.) :—

C. l.	14.5
C. b.	19
W.-L. 1 l.	24
W.-L. 2 l.	31
W.-L. 3 l.	29
W.-L. 4 l.	23
Major palm l.	17
Major palm b.	10
Antero-lat. border l.	5
Fronto-orb. border b.	12
Front b.	7

The carapace is about three-fourths as long as broad, strongly curved antero-posteriorly, with the greatest curve in front, and little curved from side to side across the greatest breadth. The surface is very finely granulated all over, more coarsely at the sides than over the gastric and intestinal regions, which are almost bare, the rest being covered with a somewhat sparse coat of small fine hairs, among which long coarse hairs arise either singly or in clumps ; the most conspicuous clumps are on the branchial regions in the grooves bounding these anteriorly.

The fronto-orbital breadth is about two-thirds the carapace breadth, and is divided by a deep median notch into two broad lobes, from each of which a deep lateral notch cuts off a tiny tooth-like lateral lobe, separated by a slight groove from the more rounded inner orbital angle.

The antero-lateral border is about one-quarter the carapace breadth, and bears three strong procurved spines, of about equal length and each consisting of a somewhat tuberculated base ending in a horny sharp smooth spine. The external angle of the orbit is sharp, consisting of a pyramidal tooth bearing several sharp spinules ; it is separated by a fissure from the lower border of the orbit, which bears a row of six fairly sharp spinules equally spaced. There are two slight crenulations in the upper border of the orbit.

The right is the major cheliped. The whole of the outer aspect of both palms is smooth except for a small area of granulation and pubescence, similar

to that on the carapace, which appears on the proximal end of the smaller. In both chelæ, the carpus is granular and pubescent, and bears a stout pointed tooth at its antero-internal angle, but it is otherwise unarmed. The meropodite bears a series of irregular bluntly procurved teeth on its lower border and two similar rather conspicuous teeth on its upper border; its outer surface is, in the main, smooth, from its lower border the line of teeth is continued on to the more proximal joints. The fingers are dark brown, the palm a very light cream or buff, the dark being separated from the cream by a line of ivory-white into which the cream fades.


The walking-legs are unarmed, except for the stout dactylus; the femur is smooth, with some long hairs, but the more distal joints are very hairy, with short and long hairs intermixed, looking under a lens not unlike a bottle-brush. The middle two legs are much longer than the others.

The species appears to be most akin to *P. fissifrons* (Stimpson, 1859, p. 36; *vide* Stimpson, 1907, p. 67, pl. viii, fig. 4).

Distribution.—Broome, W.A.

44. ACTUMNUS OBESUS (Dana, 1852).

Actumnus obesus Rathbun, 1906, p. 865, pl. xi, fig. 2.

Localities.—*a-c*, 1 ♀, 2 ♂, dredged between Pelsart Group and Rat Island; *d*, 1 ♂ (damaged), Broome, .

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>	<i>d.</i>
C. l.	8	5	10	7.5
C. b.	10	7	12	9
Fronto-orb. b.	7	4.5	8.5	6.5
Post. border of C. b.	3	3	4	3

These specimens are referred to *A. obesus* (Dana, 1852), but in some respects they approach *A. setifer* (de Haan, 1835). Rathbun's figures of her Hawaiian specimen appear to agree with *A. obesus* in regard to the carapace, and with *A. setifer* in regard to the antero-lateral teeth (*vide* Rathbun, 1906, *l. c.*). A. Milne-Edwards figures *A. setifer* with antero-lateral teeth much sharper than in my specimens (*A. Milne-Edwards*, 1865 *a*, pl. 287, pl. xviii, figs. 5 & 5 *a*, *not*, as in text, pl. xv, and as copied by Alcock, 1898, p. 202), and than specimens so labelled, in the British Museum (Natural History); of the latter those collected by Dr. Coppinger at Thursday Island (labelled 81.31) are the same as mine, while those from the Bowerbank collection (Australia, labelled 66.75) are markedly more spiny on the antero-lateral borders, and the granules are much sharper, in both respects approaching *A. Milne-Edwards*'s figure. De Haan's figure (de Haan, 1835, p. 50, pl. iii, fig. 3) agrees with that of Milne-Edwards.

The specimens agree well with Dana's description and figures (Dana, 1852, p. 244, pl. xiv, fig. 3); but the granules are not marked, and are, in fact, microscopic; the front is definitely divided medially; the antero-latera

borders are almost entire, not denticulate; the under surface of the hand and the lower part of the outer surface are, as Dana describes the carapace, granular, but with spaces between the granules filled with pubescence. Lastly, areolet 3 M (by Dana's nomenclature) is divided. Rathbun's specimen from Hawaii is figured as having areolet 3 M divided, but her specimen is much more spiny than mine or than Dana's figure, being more like *A. setifer* in this respect.

It seems possible that the two species may not be distinct and that further connecting forms will be found later.

Distribution.—Abrolhos; N. Australia; Hawaii (110); Red Sea, Persian Gulf (69); Seychelles (113).

Family GONEPLACIDÆ.

45. LITOCHEIRA BISPINOSA (Kinahan, 1856).

Litocheira bispinosa McCulloch, 1913, p. 323, *ubi* *synn.*

Locality.—1 ♀, Albany.

Measurements (in mm.) :—

C. l.	12
C. b.	15
Fronto-orbital b.	12
Front b.	7
Post. border of C. b.	7.5

Distribution.—Albany. S.W. Australia (72, 84); S.E. Australia (35, 46, 72); N. Australia (46, 84). Fiji.

McCulloch, 1913, doubts "Torres Strait" as a locality for this species, referred to by Kinahan as collected by Macgillivray at that place and kept in the British Museum. There is no specimen in the British Museum from Torres Strait, but there is one labelled "Fiji." Miers, 1884, p. 232, also gives Port Curtis as a locality.

Family PINNOTHERIDÆ.

46. PINNOTHERES EDWARDSI (de Man, 1888 a).

Pinnotheres edwardsi de Man, 1888 a, p. 103, pl. vi, figs. 6-9.

Locality.—2 ♀, Abrolhos. No locality-slip, but undoubtedly from the Abrolhos, probably escaping unnoticed from a bivalve molluscan host.

Measurements (in mm.) :—

	a.	b.
C. l.	13	12
C. b.	13	12.5

The two kinds of hairs in the pubescence, noted by Tesch (Tesch, 1918 b, p. 258), are present; the longer are readily brushed off. The blunt tooth nearer the bases of the fingers on the cheliped than the tip, which Tesch remarks,

is also seen ; it occurs as well in *P. pisum*, the chelipeds of which de Man (de Man, 1888 *a*, p. 103) states exactly resemble those of *P. edwardsi*. At the sides of the carapace the pubescence is absent, revealing a definite, though very wide, angle between the antero-lateral and postero-lateral borders. The side-walls of the carapace are more or less vertical.

Distribution.—Abrolhos. Mergui (7, 77) ; Kei Islands (130).

Family OCYPODIDÆ.

47. OCYPODE PYGIOIDES (Ortmann, 1894 *b*). (Pl. 25. fig. 1 ; Pl. 27 figs. 5, 5 *a*.)

Localities.—*a-c*, 1 ♂, 2 ♀, Wooded Island, Abrolhos, *d*, 1 ♂, Cottesloe, *e*, 1 ♂, North Beach.

Measurements (in mm.) :—

	<i>a.</i>	<i>b.</i>	<i>c.</i>	<i>d.</i>	<i>e.</i>
C. l.	24	36	32	35	24.5
C. b.	29	39	38.5	37	30
Front b.	4	6	5.5	5.5	4
Major palm b.	12.5	20	18	20.5	12.5
Stridulatory ridge l.	6	11	9	12	6

There are slight differences only from Ortmann's rather unsatisfactory figure (Ortmann, 1894 *b*, pl. xxiii, fig. 19). The sides of the carapace near the anterior angle are almost straight in the larger specimens, though slightly curved, approximating to Ortmann's figure, in the smaller. The stridulating ridge on the palm is nearly exactly half the breadth, and is therefore not as long as Ortmann figures ; nor does it start so near the lower border. In the large specimens, *b* and *d*, there is distinct groove distal to the ridge. This species, therefore, does not fit into Alcock's key (Alcock, 1900 *a*, p. 345). Either cheliped may be the larger.

In the large female *b* the carapace has become longitudinally puckered, forming grooves of which the most marked run from the middle of the upper borders of the orbits to the anterior corners of the cardiac regions.

Specimen *d* shows a tendency to puckering, and the line at which this will take place is indicated in the smaller specimens by a slightly pigmented line.

The species occurs as a sand-burrowing crab in enormous numbers on the more northerly coasts of Western Australia.

Distribution.—Abrolhos ; Cottesloe (N. of Fremantle) ; Geraldton ; Naturaliste Channel (103).

Family GRAPSIDÆ.

48. LEPTOGRAPSUS VARIEGATUS (Fabricius, 1775).

Leptograpsus variegatus Rathbun, 1917, p. 234, *ubi synn.*

Localities.—*a-d*, 1 ♀, 1 ♀ ovig., 1 ♀, 1 ♂ juv., Abrolhos Islands, *e*, 1 ♀, Sandy Island, Abrolhos ; *f-h*, 1 ♀, 2 ♂ juv., Fremantle, South Mole ; *i-k*, 1 ♀, 2 ♂, North Beach.

Measurements (in mm.) :—

	a.	b.	c.	d.	e.	f.	g.	h.	i.	j.	k.
C. l.	35.5	51	30	10.5	45	40	14.5	13	23	16.5	30
C. b.	40	59.5	33	12	51	48	17.5	14	25.5	18.5	34.5
Front b.	20	27	17	6	25	22	9	8	13	10	16
Fronto-orbital b. ...	30	41	26.5	11	36	34	15	13	21	16	26
Post. border of C. b.	17	24	12	5	20	18.5	8	6	10	8	14

In c, the second tooth of the antero-lateral border is ill-developed, thus approaching *Grapsus* (sens. strict.).

The merus-joint of the cheliped is extended anteriorly on its inner edge as a dentate lamelliform plate, somewhat as in *Geograpsus crinipes* (Dana, 1852) and *Metopograpsus messor* (Förskal, 1775).

Tesch asserts that "the species though occasionally recorded from Australia, Tasmania, and China is chiefly a West American one" (Tesch, 1918 a, p. 70, footnote). It is actually quite the most common shore-crab on the south-western coasts of Australia, and is common also at the Abrolhos, since a special note "Shore-crabs" is included with the specimens in this collection.

Distribution.—Abrolhos; N.W. Australia (46); S.W. Australia (46); S.E. Australia (36, 46, 134); ? N. Australia (46); New Zealand (80); W. America (129, 115); Shanghai (47). *Vide* also Rathbun, 1917.

49. *LEPTOGRAPSOIDES*, gen. n., *WEBHAYSI*, sp. n. (Pl. 25. fig. 5; Pl. 28. figs. 1, 1 a, 1 b.)

Localities.—1 ♀ ovig., Abrolhos Islands; 1 ♀, Long Island, Abrolhos.

Measurements (in mm.) :—

	a.	b.
C. l.	27	16
C. b.	34	20
Fronto-orbital b.	23.5	15
Front b.	11.5	7
Merus of last leg l.	13	8
" " b.	4	3
Palm l.	6	3.5
" b.	8	4

The two specimens of this new species were unfortunately lost in transit when being sent by post to the Paris Museum for comparison with the specimen believed to be the type of *Brachynotus octodentatus* (Milne-Edwards, 1837). The description is therefore made from notes already taken and not in the presence of the specimen itself. It was hoped from these specimens to clear up the doubts existing with regard to *Brachynotus octodentatus* (Milne-Edwards) and *Grapsus inornatus* (Hess, 1865), which are probably identical (*vide* de Man, 1887). The latter species has been redescribed by de Man, but the Abrolhos

specimens have not been compared with the type. Through the very kind consent of Professor Chas. Gravier, however, it has been possible to re-examine the type of Milne-Edwards's species; the Abrolhos specimens are very closely allied to this, but differ in certain small particulars. A full description is given, so that it may serve as a redescription of Milne-Edwards's species, except in the points of difference noted.

The carapace is about a third broader than long, sub-hexagonal, smooth on the posterior part except for some fine striae on the postero-lateral part of the branchial regions, but finely granular anteriorly. It is moderately convex from front to back, little convex from side to side. The branchial regions are rather swollen; the gastric region is separated from the cardiac region by a transverse depression, and, in front of the ends of this, carries a deep pit on either side near the point of junction of the hepatic, gastric, and branchial regions. The front is moderately deflexed; it tends to be produced anteriorly, and its edge is folded under as in *Leptograpsus variegatus*; the edge of the fold, however, is slightly convex upwards, not slightly convex downwards as in that species.

The epistome is broad and of varying depth, being produced up to form a triangular interantennular septum by its junction with the front; this is again as in *L. variegatus*, but again there is the difference that in that species there is a slight convexity downward, but here slightly upward. The lower edge of the epistome bordering the buccal cavern is finely granular.

The pterygostomian region and the whole of the side-wall of the body is covered by a thick pubescence.

The antero-lateral borders carry four teeth, of which the first two are strong, the last two obsolescent. These teeth are themselves microscopically serrated or granular. These serrations are present, though scarcely visible, in *B. octodentatus*.

The fronto-orbital border is about three-fifths the greatest breadth of the carapace, the front about one-third the breadth.

The orbit is bounded externally by a tooth which is the most anterior of the antero-lateral border; this tooth is pyramidal in shape with four edges, the upper two (Pl. 28. fig. 1, *a* & *b*; fig. 1 *a*, *a* & *b*) of which are the antero-lateral border and the upper border of the orbit. The other two edges (fig. 1 *a*, *c* & *d*) curve downward to be continuous with two ridges which form the lower border of the orbit. The outer ridge (fig. 1 *a*, *c*) is strongly marked, and expands into a slight protuberance on the outer side of the tooth, from which it then runs forward and medially to end on the base of a pyramidal tubercle, which is separated from the antero-lateral corner of the buccal cavern by a deep groove; in its medial part this ridge lies in the same line as the epistome. The inner ridge (fig. 1 *a*, *d*) runs down on a more medial plane to a little accessory tooth and thence onward along the floor of the orbit till it comes to lie just behind the first ridge, to end on another aspect of the same tubercle; this ridge is very small, but nevertheless distinct. From the tubercle on which these ridges

meet a third small ridge passes backward along the floor and posterior wall of the orbit, surrounding the base of the eye-stalk.

The external maxillipedes are widely gaping, showing a diamond-shaped opening between them; the ischium is much longer than the merus and bears a fringe of hairs on both medial and lateral sides; the merus is trapezoid, being narrower proximally than distally; it bears on the medial side of its outer surface a raised ridge which forms the border. There is an indication of a smaller ridge on the ischium. The exognath is slender and tapering, bears a flagellum, and is fringed with hairs.

The antennules are transversely placed in deep fossæ hidden beneath the front. The antennæ stand in the orbit, and their broad irregular basal joints limit the orbit on the medial side.

The chelipeds are equal, smooth, and slender; the merus is irregular in section and bears a few short hairs on its borders; the carpus is rounded and has a small lamellar toothed projection at the antero-internal angle, the strongest tooth being anteriorly. The hand is longer than deep, and the fingers about half as long again as the palm; each finger carries an obscure costa on its outer aspect. The fingers have very small teeth and meet for about a third of their length in a sharp ridge, which is continued round the point of the finger for a very small distance along its inner aspect, giving the appearance of a very narrow spoon at the tip.

The walking-legs are slender, the second and third being the longest and stoutest. The section of the merus is triangular, and there is a ridge of minute granules along the upper border, which terminates in a prominent spine. The dactyli and propodites carry a number of irregularly arranged, very short, stiff, black spines. The dactyli are slender, long, and slightly curved.

The female abdomen is broadly circular, but the last joint has a median projection forward, which distorts the circle, making the joint not a segment of the circle.

The colour in spirit is a dirty yellow mottled with red in patches: there are discontinuous rings of a similar dull red on the merus, carpus, and propodus of the legs.

From comparison with the specimen which is believed by Professor Gravier to be the type of *Brachynotus octodentatus* (Milne-Edwards) the following points of difference appear. In the latter,

(a) there is no border, corresponding to fig. 1 a, c, on the antero-lateral tooth running down to a protuberance on the outer angle of the orbit; instead the outer angle is open, smooth, and rounded;

(b) the interorbital ridge corresponding to c does not run as far laterally as in *L. webhaysi*, but stops short before it turns upward;

(c) the ridge corresponding to d is distinctly granular, not smooth as in *L. webhaysi*;

(d) the superior border of the orbit, strongly granular in *L. webhaysi*, is scarcely granular;

(e) the groove on the pterygostomian region and the pit at the outer angle of the epistome are not so deep ;

(f) the pits on the back are not so deep ;

(g) the toothed lamellar plate on the carpus is less broad and less projecting.

The description given by de Man of *Grapsus inornatus* (Hess) shows that this species differs from both of the above in,

(a) having the claws scarcely toothed (untoothed, according to Hess) ;

(b) having some sharp granules on the inner angle of the carpus, instead of the toothed lamellar plate of the other two. The character of the ridges running from the outer orbital tooth is not stressed by de Man, so that it is impossible to make the comparison without reference to the type, which is in the collection of the Gottingen Museum.

Dr. J. G. de Man, in a very kind and helpful personal communication, points out that Miss Rathbun in her key to the subfamilies and American genera of the Grapsidae (Rathbun, 1917, p. 225) divides those in which the antennulae fold beneath the front in the ordinary way and in which there is no oblique hairy ridge on the exposed surface of the external maxillipedes into two subfamilies, the Grapsinae and the Varuninae ; in the former the lower border of the orbit runs downward toward the buccal cavern ; in the latter, " the lower border of the orbit does not run downward toward the buccal cavern, but is supplemented by a rather distant sub-orbital crest, which is in line with the anterior border of the epistome." Dr. de Man remarks that in *Leptograpsus marmoratus* (Fabricius), a representative of the first group, " the finely granulated lower border of the orbits extends to the antero-external angle of the buccal cavern, curving medially toward that angle and there is no trace of a sub-orbital crest posterior to the lower border." In the Japanese *Brachynotus sanguineus* (de Haan), however, " one observes a smooth orbital crest, that is transversely striated, immediately posterior to the finely granulated lower border of the orbit ; this crest, in line with the granulated border of the epistome, extends, gradually narrowing, to the middle of the 2nd antero-lateral tooth of the carapace."

In *L. webhaysi*, it will be noted that there is no suborbital crest in the sense of the above ; but it is possible that the ridge *c* represents it and the ridge *d* is the true lower border of the orbit ; the former, however, certainly does not run up to the second antero-lateral tooth, nor is it posterior to the ridge *d*. Dr. de Man writes that he considers it justifiable, in the absence of a suborbital crest, to regard this species as belonging not to *Brachynotus* (Varuninae) but to a new genus of the Grapsinae, and most closely related to *Leptograpsus*. The name *Leptograpsodes* is suggested to include the three species *L. octodentatus* (Milne-Edwards), *L. inornatus* (Hess), which may be identical, and *L. webhaysi* (sp. n.). The description of *L. inornatus* by de Man differs from the Paris Museum specimen of *L. octodentatus* in having coarse granules on the carpus instead of a lamellar toothed plate, and in having untoothed claws. The habitat of these two is Eastern Australia ; while *L. webhaysi* is Western Australian.

50. *PLANES MINUTUS* (Linnæus, 1758).

Locality.—a-g, 3 ♂, 4 ♀, Cottesloe Beach.

In bank of seaweed left by storm, July 1919.

There is great variation in carapace colour and pattern, and in the size of the postocular tooth. Though almost universal, this species does not appear in Alcock's Indian fauna (Alcock, 1900) nor in Laurie's Ceylon report (Laurie, 1906) nor in the Persian Gulf (Nobili, 1906).

Distribution.—Almost universal, pelagic.

51. *CYCLOGRAPSPUS AUDOUINII* (H. Milne-Edwards, 1837). (Pl. 25. fig. 3 ; Pl. 27. fig. 6.)

Cyclograpsus audouinii H. Milne-Edwards, 1837, p. 78.

Cyclograpsus lavauxii H. Milne-Edwards, 1853, p. 197.

Cyclograpsus lavauxii Haswell, 1882 c, p. 103, *et synn.*

Cyclograpsus lævis Hess, 1865, p. 152.

Cyclograpsus audouinii de Man, 1887, p. 700 ; 1896, p. 352 ; Tesch, 1918 a. p. 126, *ubi synn.*

Locality.—3 ♂, North Beach.

Measurements (in mm.) :—

	a.	b.	c.
C. l.	14.5	18	11
C. b.	18	22.5	14
Fronto-orbital b.	13	16	10
Front b.	7	8	6
Post. border of C. b.	7.5	9	7

Hess describes this species as *C. lævis* (Hess, 1865), and states it to be very near *C. cinereus* (Dana, 1852) and perhaps not to be distinguished. From material in the British Museum (Natural History) the two species appear to be separable as follows :—(i) the abdomen of the male in *C. cinereus* has parallel edges, in *C. audouinii* convergent and slightly sinuous edges ; (ii) in *C. cinereus* (Pl. 27. fig. 7) the lateral edges of the carapace overhang the side-wall, forming a groove which bears a line of sparse hairs ; in *C. audouinii* the overlap is not sufficient to form a gutter, and the line of hairs is thick and regular ; (iii) there is a ridge of teeth beneath the orbit in both species. In *C. cinereus* this ridge is irregularly toothed, and continues as a beaded ridge on to the pterygostomian region ; starting medially, it inclines upward but quickly turns laterally and horizontally ; in *C. audouinii* the teeth are regular, the ridge is straight and horizontal, and is continued on the pterygostomian region as a few regular rounded teeth, not as a continuous ridge ; (iv) the outer angle of the orbit is produced downwards in *C. cinereus* so that it forms an almost complete side-wall to the orbit ; in *C. audouinii* the outer angle reaches barely to the upper part of the fully retracted eye, and the orbit is fairly open laterally.

Distribution.—Cottesloe (near Fremantle, S.W. Australia) ; S.E. Australia (46, 129) ; New Guinea (129) ; New Zealand (80, 129).

Family PLAGUSIIDÆ.

52. PERCON PLANISSIMUM (Herbst, 1804).

Liolophus planissimus Alcock, 1900 a, p. 439, *et synn.**Percnon planissimum* Rathbun, 1900, p. 281; 1906, p. 842, *et synn.**Locality*.—*a-b*, 2 ♀, Long Island, Abrolhos.*Measurements* (in mm.) :—

	<i>a.</i>	<i>b.</i>
C. l.	22	32
C. b.	20	29
Post. border of C. b.	10	15
Fronto-orb. b.	13	17
Epistome b.	5.5	7
W.-L. 3 l.	45.5	65

Distribution.—Abrolhos. " West India region. Oriental region to Japan and Sandwich Islands. Clarion Island. Cape St. Lucas. Chile. Azores. West coast of Spain and Portugal. West and South Africa " (Rathbun, 1906). N.W. Australia (46); S.W. Australia (46); S.E. Australia (31, 46); N. Australia (46, 84); New Zealand, Norfolk Island (37, 80); Fiji, Funafuti (16, 135); Hawaii (110); N.E. Malay (76); S.W. Malay (7); Christmas Island (24); India, Ceylon (7); Maldives, Laccadives (7, 19); Red Sea, Persian Gulf (69); Seychelles (113); S. Africa (124).

53. PLAGUSIA CAPENSIS (de Haan, 1835).

Plagusia chabrus Haswell, 1882 c, p. 111.*Plagusia capensis* Stebbing, 1905, p. 47, *ubi synn.**Plagusia capensis* Tesch, 1918 a, p. 129, *ubi synn.**Locality*.—Part of carapace; 1 cheliped. North Beach.

A fairly common species on South-Western Australian coasts.

Distribution.—S.W. Australia; S.E. Australia (35, 37, 46, 118); New Zealand (80); S. Africa (124); Tonga (129). Juan Fernandez, Chile (129).

54. PLAGUSIA DEPRESSA (Fabricius, 1775) var. TUBERCULATA (Lamarek, 1818). (Pl. 27. fig. 8.)

Plagusia depressa var. *squamosa* Alcock, 1900 a, p. 437, *et synn.**Plagusia depressa* var. *tuberculata* Rathbun, 1906, p. 841, *synn.* 1917, p. 234; Tesch. 1918 a, p. 128.*Localities*.—*a*, 1 ♂, Abrolhos Islands; *b*, 1 ♀, Long Island, Abrolhos.*Measurements* (in mm.) :—

	<i>a.</i>	<i>b.</i>
C. l.	12.5	23
C. b.	13	25
Post. border of C. b.	6.5	13
Fronto-orb. border b.	10	16
Epistome b.	4.5	8.5
W.-L. 3 l.	26	48

Miers (1878, p. 149) distinguishes an Atlantic form *P. depressa* (Fabricius, 1775) from an Indian form, *P. tuberculata* (Lamarck, 1818), by the dentate coxal process; he is uncertain with regard to *P. squamosa* (Herbst, 1790). Hilgendorf (1882, p. 24) takes *P. tuberculata* as a synonym of *P. squamosa*, claiming to have examined Herbst's type, and is followed by other authors who style the form with entire coxal process *P. depressa* var. *squamosa* (vide Alcock, 1900 a, p. 437). Rathbun (1906, p. 841), citing Hilgendorf, considers that a doubt exists with regard to the identity of *P. squamosa* (Herbst), and will not accept it as a type, referring to the variety as *P. depressa* var. *tuberculata* (Lamarck). There is no reason to doubt, however, that *P. squamosa* (Herbst, 1790, p. 260, pl. xx, fig. 113) is a form with dentate coxal process and identical with *P. depressa* (Fabricius) and *P. depressa* (Herbst, 1790, p. 117, pl. iii, figs. 35 a-b). The only reasons for considering it otherwise are (a) the locality given "East Indies" which should be the habitat of the form with the entire coxal process, (b) the colour, which Herbst uses to separate his two species, and (c) the misreading by Hilgendorf of Herbst's description. The locality cannot be considered a valid criterion, as the Atlantic form with dentate coxal process has since been described by many observers from the Indian Ocean.

The colour, likewise, is very variable. Herbst's original description of *P. squamosa* reads "Die Füsse haben rothe Banden und Flecken, und auf den Hüften steht eine Längsbinde, die an den Seitenrändern blumenförmig ausgezackt ist, und das Asehen von Bildhauerarbeit hat; sie wird eigentlich durch zwey kleine [*sic*=kleine ?] breite etwas vertiefte Furchen oder Streifen gebildet, die wegen der kleinen Härchen, womit sie überzogen sind, eine graue Farbe bekommen. Der innere Rand der Hüften hat eine kielförmige Erweiterung, die oberhalb in einen spitzigen Zahn ausläuft." Hilgendorf claims to have examined Herbst's types in the Berlin collection; he refers to "der Beschreibung Herbst's, der 'einen' spitzigen Zahn' auf der Huft erwähnt," adding that this does not agree with the figure (pl. xx, fig. 113) and that the type agrees with the text. He appears to have taken "Huft" to mean "coxa," whereas it obviously refers to the meropodite or "femur"; if it refers to the coxa, then Herbst's description of "Längsbinde" with a "flower-like sculptured appearance formed by two small gutters filled with little hairs" has no meaning; the femur, however, is well fitted by the description, the sharp spine being that which is present on both Atlantic and Indian forms on the anterior border ("innere Rand") at its distal end; this is indicated in Herbst's short description of *P. squamosa* by the phrase "*femoribus unidentatis*" (cf. Pl. 27. fig. 8).

There is nothing in Herbst's description, therefore, to indicate that the coxal processes are entire, whereas his figure shows them to be dentate. Clearly, Herbst's species is identical with *P. depressa* (Fabricius), and the form with the entire coxal process was unknown to him; for the latter, Lamarck's name *P. tuberculata* must stand. Should a re-examination of the type of *P. squamosa* (Herbst) confirm Hilgendorf's observation that the coxal process is entire,

one will have to assume that a mistake was made by the artist who drew Herbst's figure, and also that Herbst, in seeking to differentiate the two forms, overlooked this rather obvious point in his description, though remarking on the dentate coxal process in *P. depressa* (Fabricius). A more natural assumption would be that the specimen examined by Hilgendorf was not the type of Herbst.

Of the Abrolhos specimens the small male *a* has the epistome cut into three lobes only, the female *b* having the normal seven lobes ; this lobation is probably a growth-change.

The chelipeds are small and very little tuberculated ; those of the young male are in all respects similar to those of the female. They show, instead of the transverse tubercles on the outer side of the hand, a reticulated marking only visible under a lens ; the inner angle of the wrist might be described as "coarsely dentiform" (Alcock, 1900 *a*, p. 438), but, in addition, is almost hidden in a mass of stiff bristles. Possibly, the chelipeds in this species exhibit facultative dimorphism (for *cf.* Alcock, *l. c.*).

Distribution.—Abrolhos : "Cape St. Lucas. Throughout Oriental region, from the Hawaiian Islands westward and southward to Japan and the Arabian Sea" (Rathbun, 1917). S.E. Australia (46) ; Hawaii (110) ; N.E. Malay (112) ; India, Ceylon (7) ; Maldives and Laccadives (19) ; Red Sea, Persian Gulf (69) ; Seychelles (113) ; S. Africa (124).

Family CORYSTIDÆ.

55. Genus et species indeterminata.

Locality.—1 ♂, Abrolhos.

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EXPLANATION OF THE PLATES.

PLATE 24.

- Fig. 1. *Thalamita prymna* var. *proxima*, var. nov., dorsal view. × 1.
2. *Thalamita prymna* var. *pelsarti*, var. nov., dorsal view. × 1.
3. *Thalamita dakini*, sp. n., dorsal view. × 2.
4. *Thalamita macropus*, sp. n., dorsal view. × 2.

PLATE 25.

- Fig. 1. *Ocypode pygoides* (Ortmann, 1894 b), dorsal view. × 1.
2. *Pilumnus pulcher* (Miers, 1884), dorsal view. × 1.
3. *Cyclograpsus audouinii* (H. Milne-Edwards, 1837), dorsal view. × 1.
4. *Dromidiopsis abrolhensis*, sp. n., dorsal view. × 1.
5. *Leptograpsoides*, gen. n., *webbaysi*, sp. n., dorsal view. × 1.

PLATE 26.

- Fig. 1. *Pilumnus granti*, sp. n., dorsal view, $\times 2$; 1 *a*, cheliped, outer aspect, $\times 2$.
 2. *Pilumnus maccullochi*, sp. n., dorsal view, $\times 2$; 2 *a*, cheliped, outer aspect, $\times 2$.
 3. *Actaea levidorsalis*, sp. n., dorsal view, $\times 2$; 3 *a*, cheliped, outer aspect, $\times 2$; 3 *b*, last walking-leg, $\times 2$; 3 *c*, 3rd walking-leg, $\times 2$.

PLATE 27.

- Fig. 1. *Pilumnus edamensis* (de Man, 1888 *b*), carapace, $\times 2$; 1 *a*, cheliped, $\times 2$.
 2. *Elamene truncata* (Stimpson, 1858), ♂, abdomen, $\times 2$.
 3. *Halimacarcinus bedfordi*, sp. n., carapace, $\times 8$; 3 *a*, buccal and antennal region, $\times 8$; 3 *b*, last walking-leg, $\times 8$.
 4. *Halimacarcinus australis*, carapace, $\times 2$; 4 *a*, anterior aspect, front, orbits, and antennal region, $\times 2$.
 5. *Ocypode pygoides* (Ortmann, 1894 *b*), orbit, $\times 2$; 5 *a*, inner surface, major cheliped, $\times 2$.
 6. *Cyclograpsus audouinii* (H. Milne-Edwards, 1837), orbit, $\times 3$.
 7. *Cyclograpsus cinctus* (Dana, 1852), orbit, $\times 3$.
 8. *Plagusia depressa* var. *tuberculata* (Lamarck, 1818), last walking-leg, outer aspect, $\times 2$.

PLATE 28.

- Fig. 1. *Leptograpsodes*, gen. n., *uebhaysi*, sp. n., carapace, $\times \frac{1}{2}$; 1 *a*, fronto-orbital region, $\times 2$. *a*, ridge from external orbital angle continuous with antero-lateral border; *b*, ridge continuous with supraorbital border; *c*, ridge continuous with infra-orbital border; *d*, fourth ridge in lower part of orbit. 1 *b*, cheliped, $\times 3$.
 2. *Thalamita macropus*, sp. n., carapace, $\times 2$; 2 *a*, front orbits, and antero-lateral borders, $\times 2$.
 3. *Thalamita prymna* var. *palsarti*, var. nov., carapace, $\times 1$; 3 *a*, fronto-orbital region and antero-lateral border, ventral view, $\times 2$.
 4. *Thalamita dakini*, sp. n., fronto-orbital region and antero-lateral borders, dorsal view, $\times \frac{1}{2}$.

PLATE 29.

- Fig. 1. *Thalamita prymna* var. *proxima*, var. nov., anterior half of carapace, $\times 1$; 1 *a*, fronto-orbital region and antero-lateral border, ventral view, $\times 2$.
 2. *Thalamita sima* (Milne-Edwards, 1834), cheliped outer aspect, $\times 2$.
 3. *Cryptodromia tumida* var. *spinifera* var. nov., anterior half of carapace, $\times 4$; 3 *a*, genital ridges of ♀, $\times 3$; 3 *b*, last walking-leg, $\times 2$.
 4. *Cryptodromia tumida* (Stimpson, 1859), carapace, $\times \frac{3}{2}$; 4 *a*, antero-lateral and fronto-orbital borders, $\times 4$.

PLATE 30.

- Fig. 1. *Dromidiopsis abrolhensis*, antero-lateral and fronto-orbital borders, dorsal view, $\times 2$; 1 *a*, cheliped, ventral view, $\times 2$; 1 *b*, carapace, front view, $\times 2$; 1 *c*, cheliped, $\times 1$. In all figs. - *a*, lateral tooth of front; *b*, middle tooth of front; *c*, supraorbital lobe; *d*, bay between outer orbital angle and first antero-lateral tooth; *e*, separate tooth in infraorbital border; *f*, outer orbital angle; *h*, first anterolateral tooth; *j*, second antero-lateral tooth; *k*, third antero-lateral tooth; *l*, fourth antero-lateral tooth.

Notes on the Segmental Excretory Organs of Crustacea.—V. On the Maxillary Glands of the Syncarida. By S. M. MANTON, M.A., Ph.D., F.L.S., Demonstrator in Comparative Anatomy in the University of Cambridge and Fellow of Girton College.

(With 2 Text-figures.)

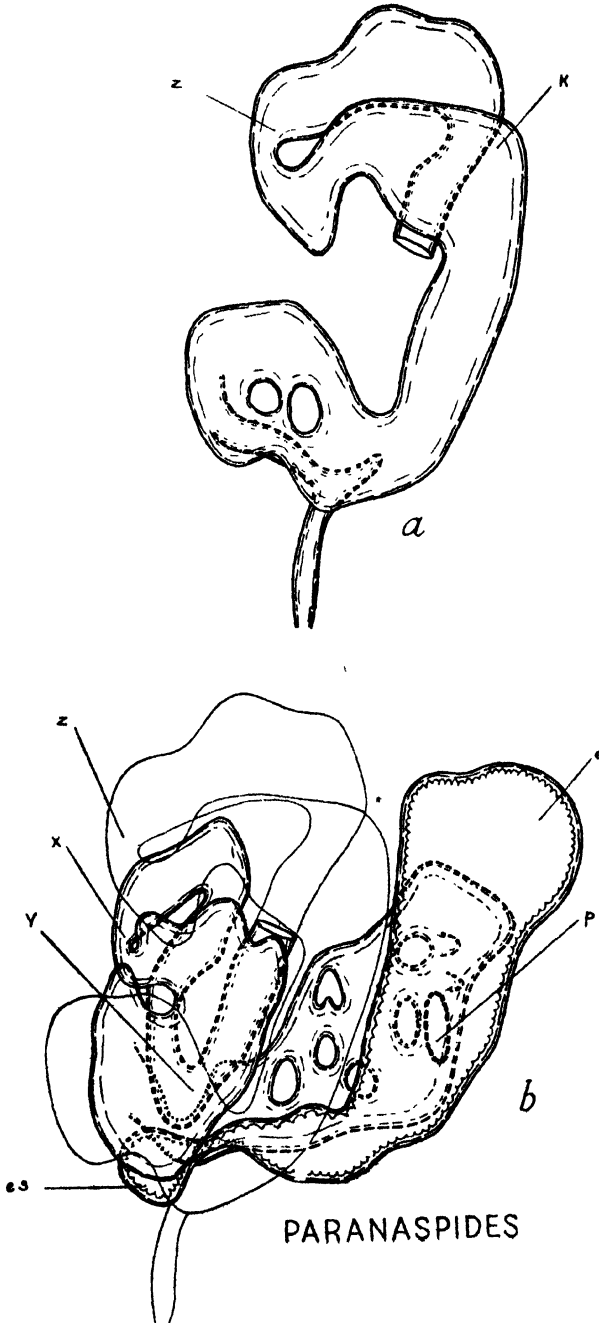
[Read 6th March, 1930.]

AMONG the Syncarida the maxillary glands of *Anaspides* and *Bathynella* have already been described (Cannon and Manton, 1927, Chappuis, 1915). The diagrammatic reconstruction of the gland of *Anaspides* (Cannon and Manton, fig. 2, p. 443) was made from slightly oblique sections of uncertain thickness, and was intended merely to show the main pattern of the duct-looping for comparison with that of *Chirocephalus*. Fresh material was obtained on a visit to Tasmania during 1929, and detailed reconstructions of the maxillary glands of *Anaspides*, *Paranaspides*, and *Koonunga* have been made.

The general disposition of the coils of the efferent duct of the maxillary gland in *Paranaspides*, *Anaspides*, and *Koonunga* is similar. Owing to the coils being in all cases considerably superimposed, parts of the ducts are drawn separately in text-fig. 1 *a*, *c* & *e*, while the deeper coils and end-sac are shown in text-fig. 1 *b*, *d* & *f*. The efferent duct shows two homologous loops, X and Z, lying in the upper anterior part of the gland. The points X and Z are connected by a loop passing through the point Y, while from X the duct passes to the end-sac and from Z to the exit on the maxilla (text-fig. 2).

The details of the coils of the gland may now be considered. The duct from its opening on the maxilla runs upwards and forwards forming an S-shaped bend—(P in text-fig. 2)—in all three animals, but in *Koonunga* this bend is very much smaller than it is in *Paranaspides* and *Anaspides*. The duct then passes upwards to the bend Z, forming an angle K on the way. The bend K is most fully developed in *Koonunga*. From Z the duct loops downwards to the point Y and upwards to X. In *Paranaspides* the loop to Y is very long, in *Anaspides* it is shorter and in *Koonunga* it is hardly formed at all. From X the duct reaches the end-sac in *Paranaspides* by way of a simple S-shaped twist. In *Anaspides* and *Koonunga* the middle part of the S-shaped loop has been folded so that the duct crosses over itself at A before reaching the end-sac. The position of this folding, however, is not quite the same in the two. In *Koonunga* it has been caused by an outward and backward fold of the duct, while in *Anaspides* the folding has been inwards and forwards. The duct in *Paranaspides* is fenestrated and presents several blind projections, mainly

TEXT-FIG. 1 (first part).



Reconstructions of the maxillary glands of *Paranaspides*, *Anaspides*, and *Koonunga*. The exit tube and superficial coils of the duct are shown in figures *a*, *c*, and *e*, while the deeper coils of the duct are shown in figures *b*, *d*, and *f*, the thin lines representing the positions of the superficial coils. *e.s.*, end-sac; *p.*, opening between end-sac and duct; *K*, *X*, *Y*, and *Z*, homologous points on the ducts.



Fig. 1



Fig. 3



Fig. 2



Fig. 4



Fig 1



Fig 2



Fig 3

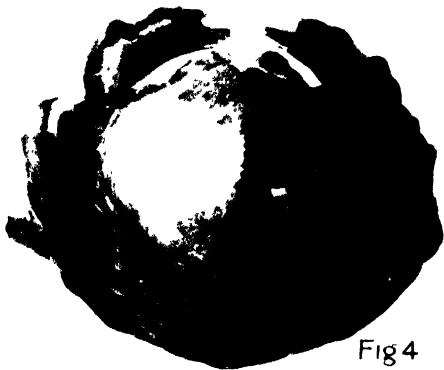


Fig 4

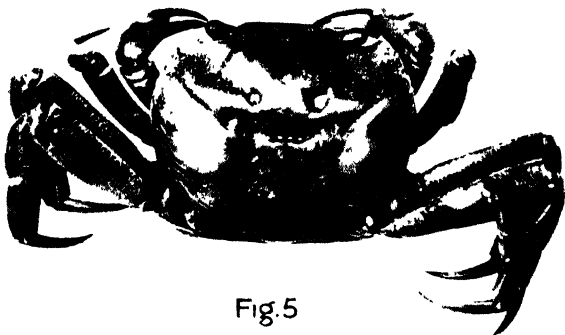
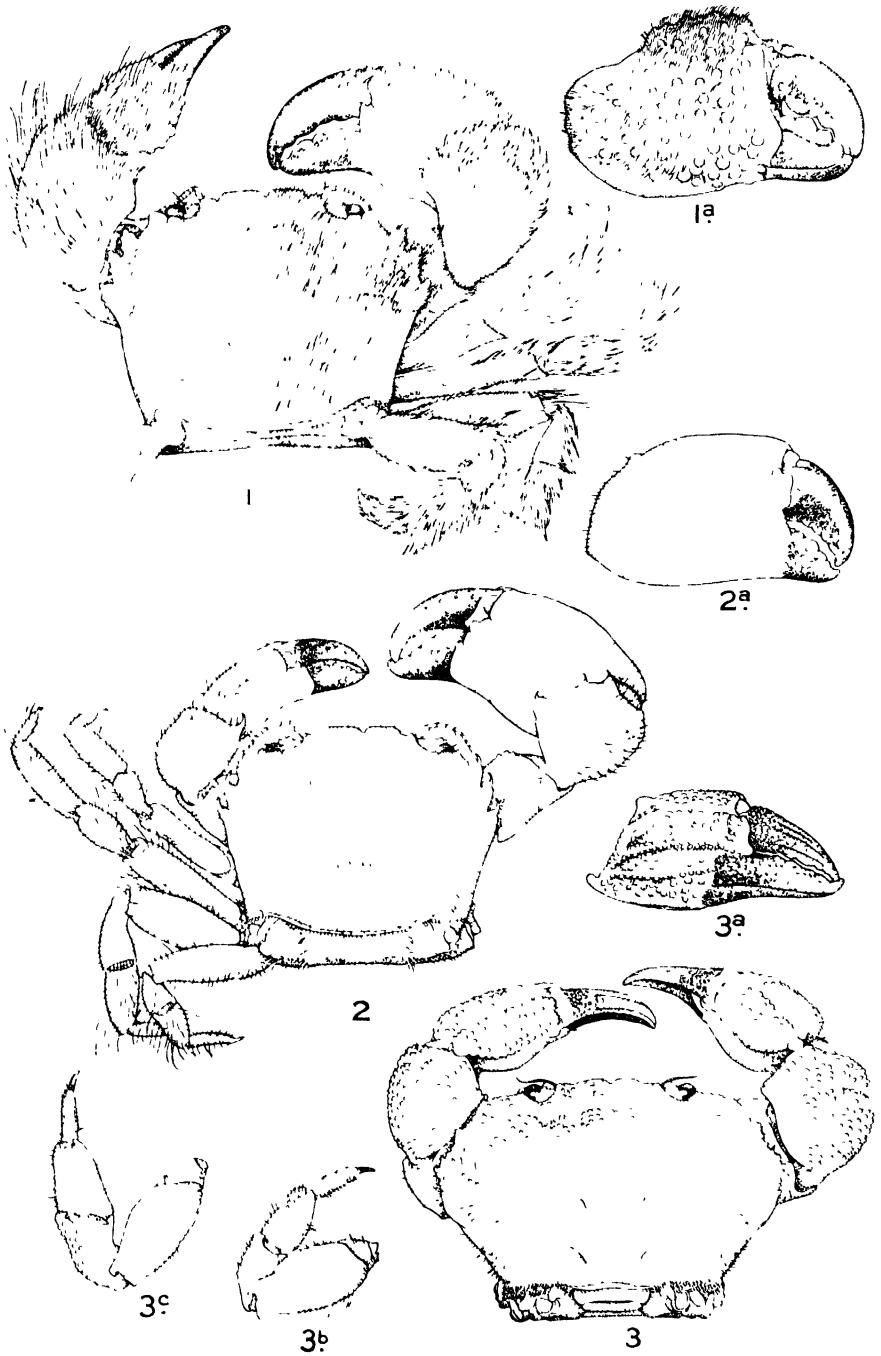
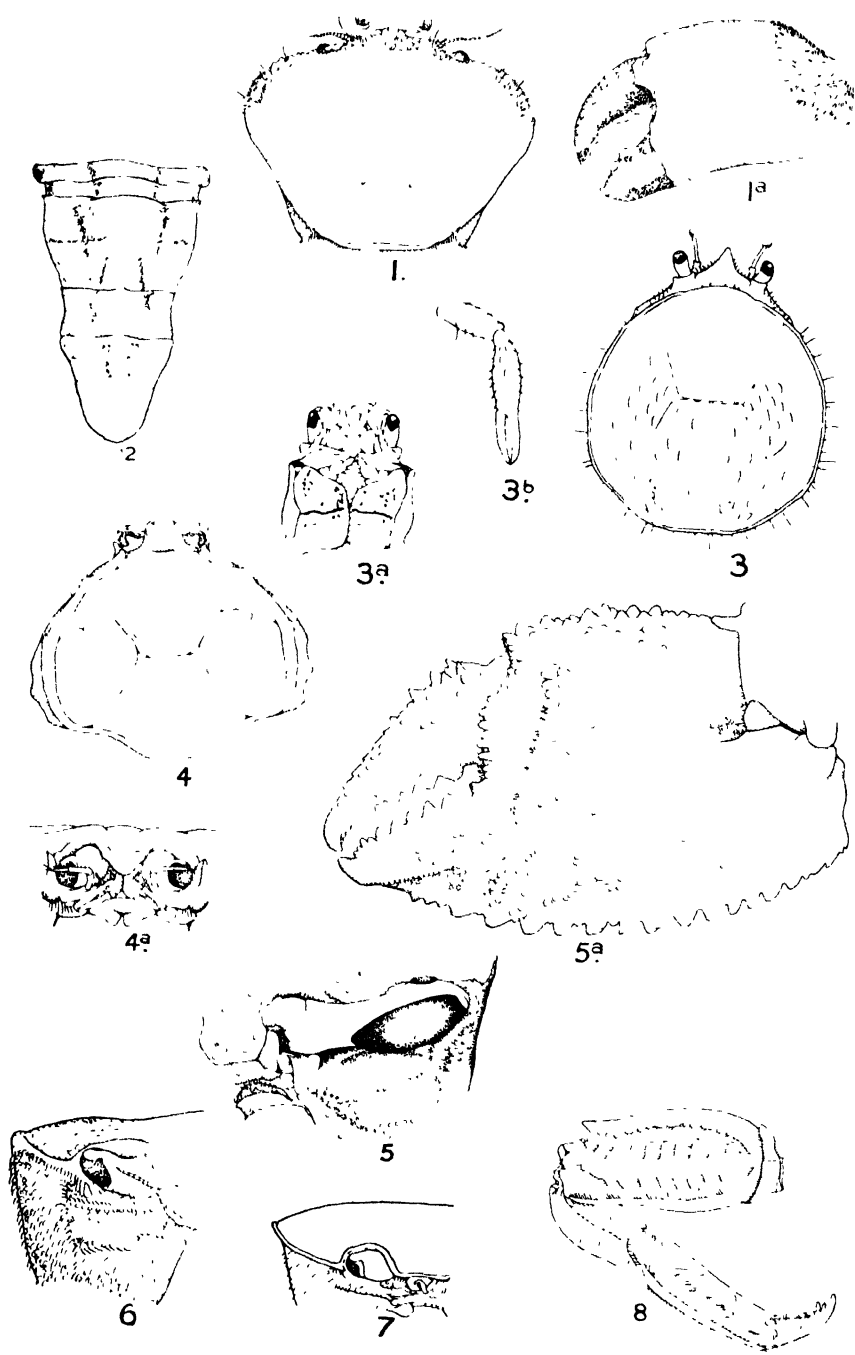
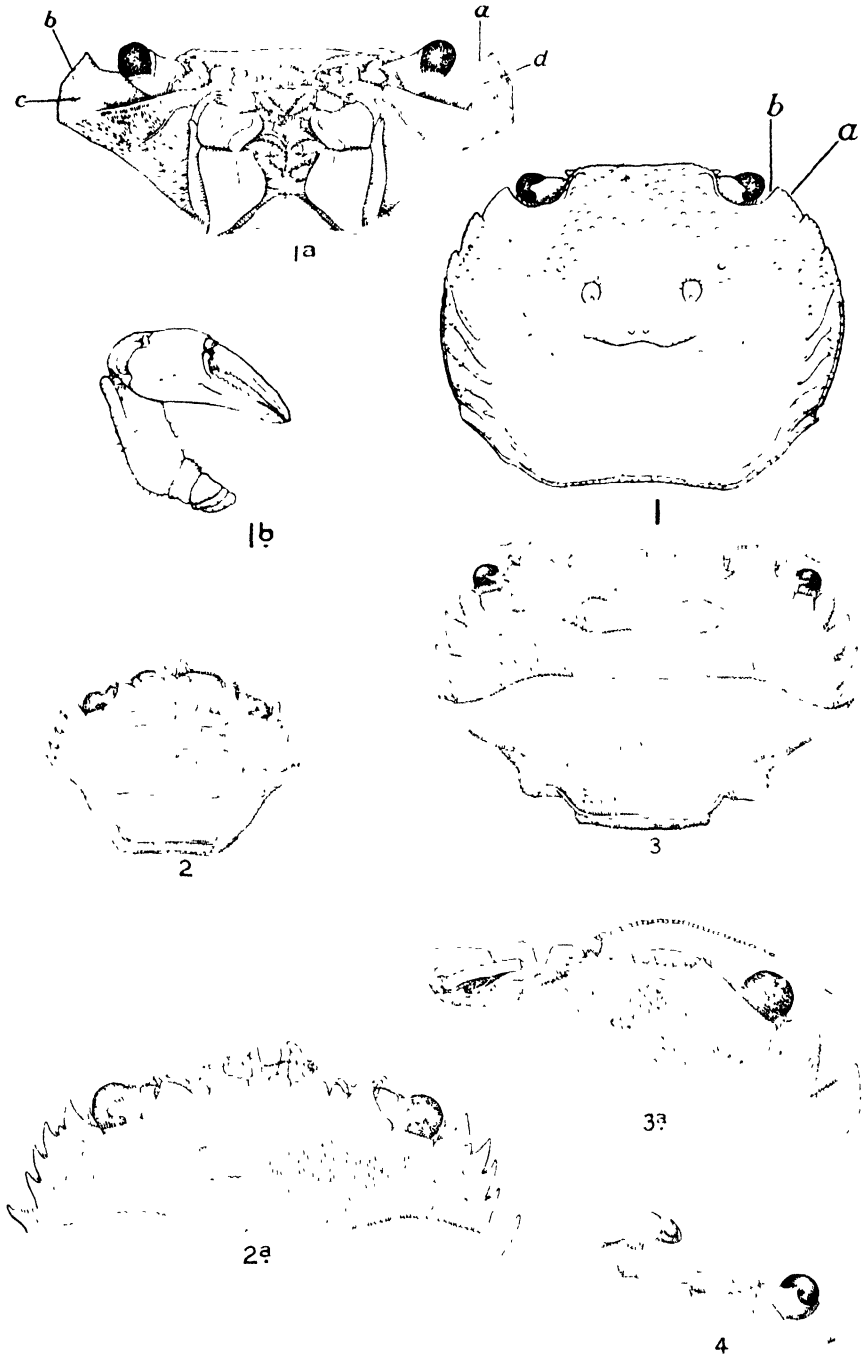


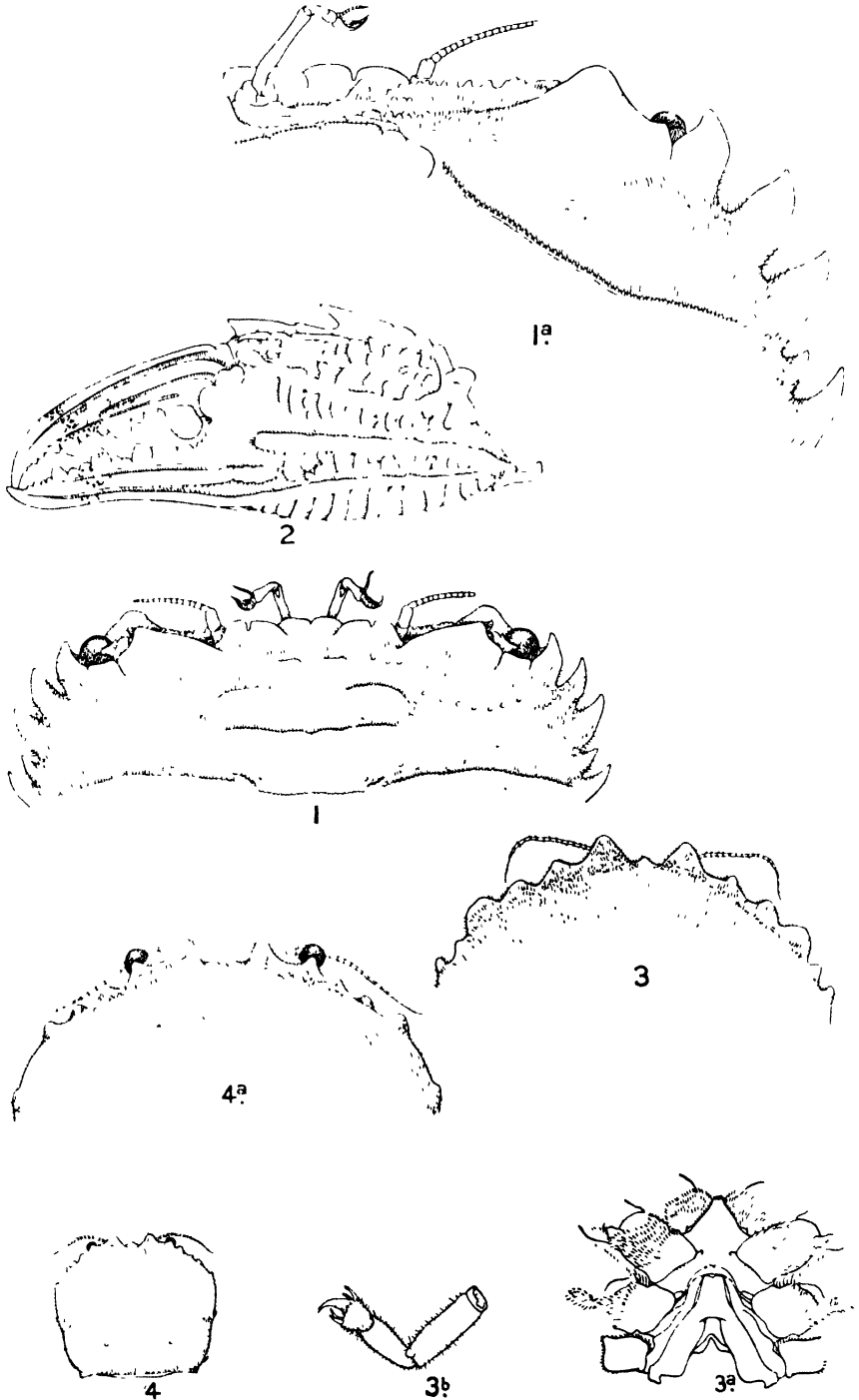
Fig. 5



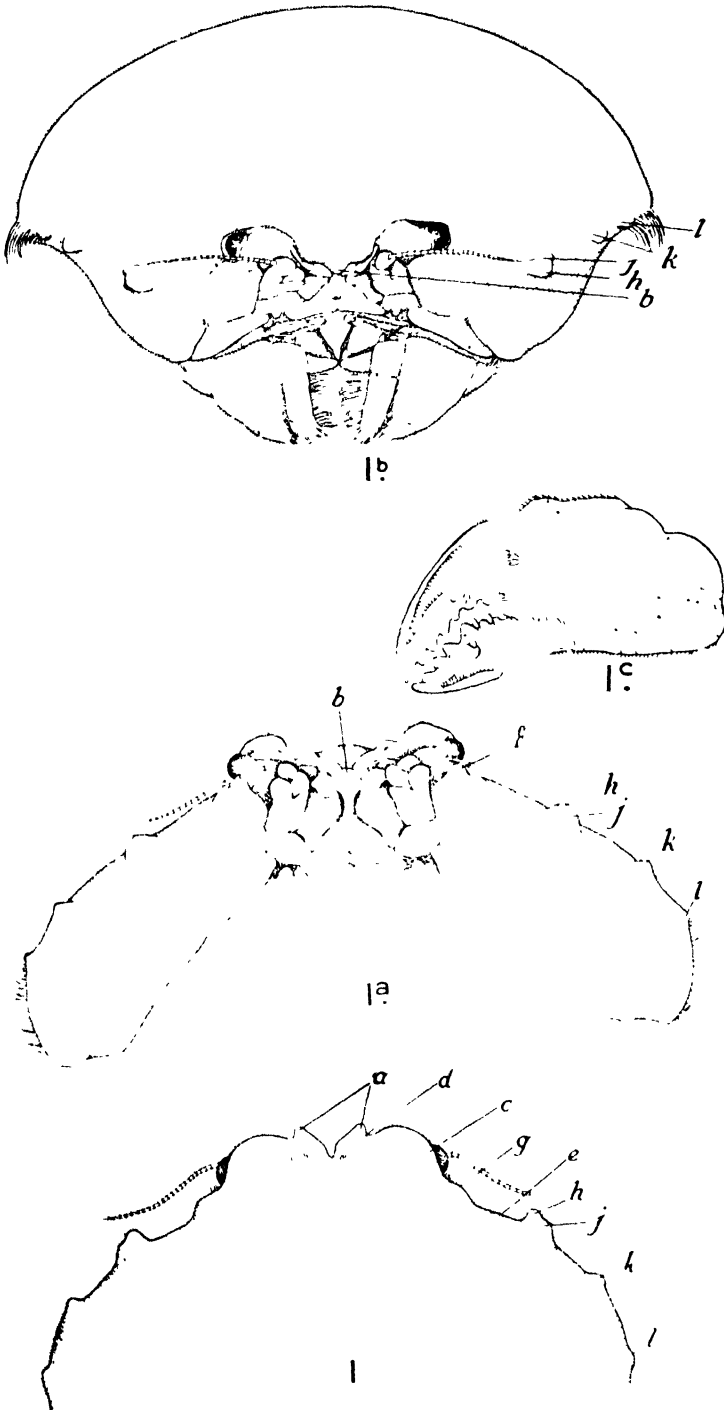


CRUSTACEA BRACHYURA OF THE ABROLHOS ISLANDS.



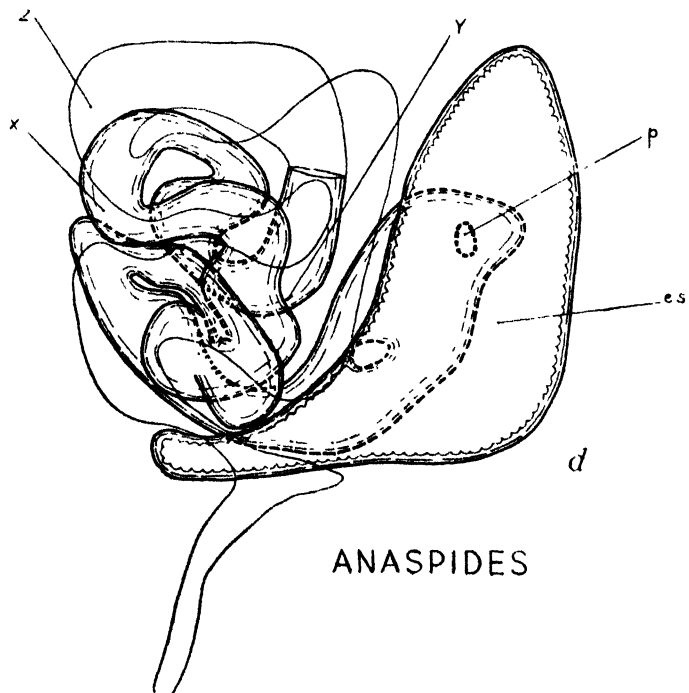
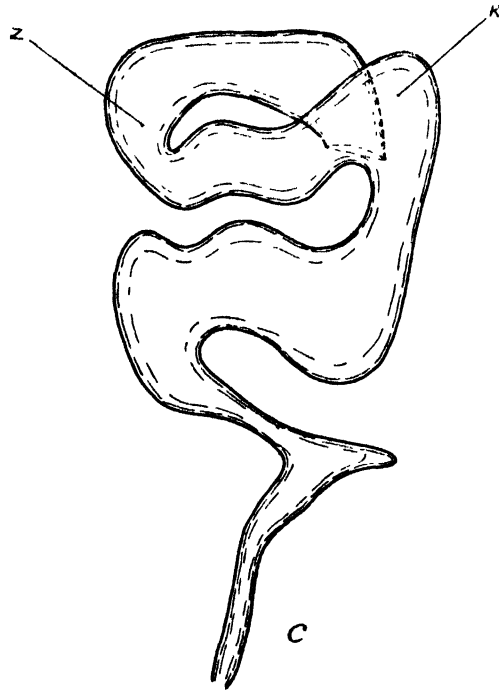


CRUSTACEA BRACHYURA OF THE ABROLHOS ISLANDS.



CRUSTACEA BRACHYURA OF THE ABROLHOS ISLANDS.

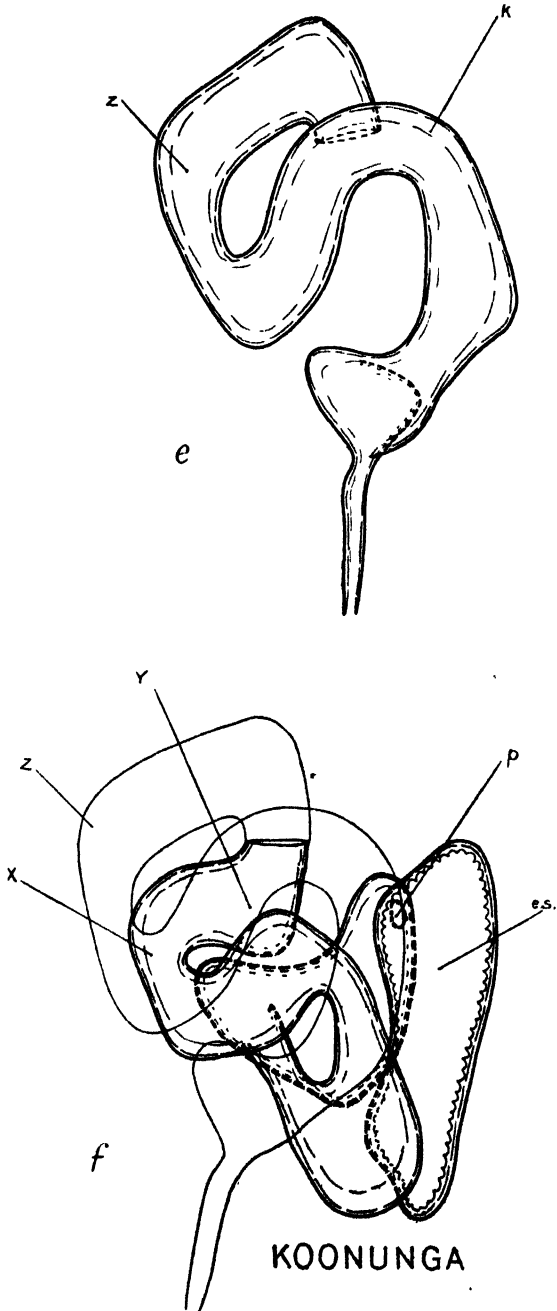
TEXT-FIG. 1 (second part)



ANASPIDES

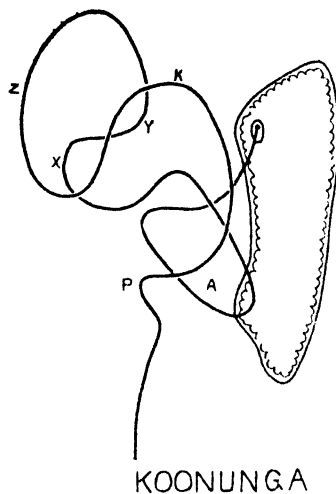
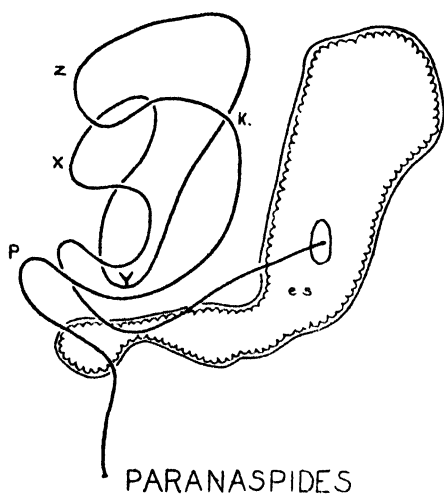
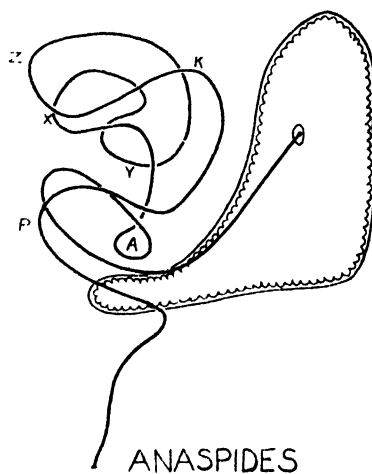
[For legend, see previous page]

TEXT-FIG. 1 (third part).



[For legend, see p. 468.]

TEXT-FIG. 2.



Diagrams showing the plan of the looping of the ducts of the maxillary glands of *Paranaspides*, *Anaspides*, and *Koonunga*.

located near the end-sac and near the exit (text-fig. 1 b). In *Anaspides* a single fenestration is present through the duct near the end-sac (text-fig. 1 d). These fenestrations resemble those found through the end-sac in certain Branchiopoda.

The end-sacs of *Paranaspides* and *Anaspides* are relatively larger than that of *Koonunga*, and communicate with the duct by a simple opening which is very large in *Paranaspides*. The cells bounding this opening in *Paranaspides* are swollen and project into the lumen much as do the "valve" cells of *Anaspides* already described (Cannon and Manton, 1927), but the large size of the opening between end-sac and duct in *Paranaspides* precludes these cells from exercising a valvular function unless the region is very contractile. No muscle-fibrils could be detected around the opening. The fixation of *Koonunga* did not allow of a detailed examination of the junction of the end-sac and duct.

A comparison of the maxillary glands of *Paranaspides*, *Anaspides*, and *Koonunga* shows a close resemblance between *Paranaspides* and *Anaspides* in the positions of the duct and end-sac. Loops P and Y are well formed in both, and the end-sac is of a similar shape. Loop Y shows progressive reduction passing from *Paranaspides* to *Anaspides* and *Koonunga*. The ducts of *Anaspides* and *Koonunga*, however, resemble each other in possessing a loop A. This loop has not been formed in the same manner in the two animals and was probably independently acquired from some form without this loop. The pattern of duct shown by *Anaspides* and *Koonunga* could have been derived from a type resembling that of *Paranaspides* in general form, but lacking its peculiar features of excessive duct fenestration, and perhaps, the extended loop Y. Such a conception of the inter-relationships of the glands in the three types is in harmony with conclusions on the affinities of the three animals based upon external anatomy and habits.

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Microspides calmani, a new Syncaridan from the West Coast of Tasmania

By GEORGE E. NICHOLLS, D.Sc., A.R.C.S., F.L.S.

(PLATES 31 & 32, Map, and 1 Text-figure.)

[Read 7th November, 1929.]

IN the summer of 1907-08, the late Geoffrey Smith visited Tasmania for the purpose of collecting and studying the Freshwater Crustacea. Till that time, as he notes (1909 *a*, p. 61), this freshwater fauna had remained practically unknown, except for the brief description of a few species by G. M. Thomson (1893), in which paper that author announced his discovery of *Anaspides*.

Smith's visit resulted in the discovery of a number of new Malacostracan forms of considerable interest, including a second Syncarid (*Paranaspides*) and new species of *Phreatoicus* and *Neoniphargus*. In his paper he suggests that the island is divisible into three distinct regions: (1) a Central Plateau, rich in genera and species of Crustacea, (2) a Northern Region, from which the characteristic forms (*Anaspides*, *Phreatoicus*, and *Neoniphargus*) were apparently absent, and (3) the West Coast Region, a region of heavy rainfall, only into the upper corner of which Smith seems to have penetrated.

In his book 'A Naturalist in Tasmania,' however, he remarks that "both in its physical and faunistic characters [the West Coast Region] is more closely allied to the Northern Area than to the Greenstone Plateau," suggesting that he had found the Freshwater Crustacea lacking—and, indeed, he records specimens only from two localities.

From this region had come, however, in 1901, a few specimens of that remarkable Phreatoicid, *Hypsimitopus intrusor* Sayce, and in January 1928 I took advantage of a visit to Hobart to make a hasty trip to the West Coast in the hope of rediscovering this species, in which attempt I was wholly unsuccessful. I was, however, altogether unprepared for the variety and abundance of the freshwater and semi-terrestrial Amphipodan fauna, and it was while engaged in collecting these that I chanced upon the very small Syncarid which forms the subject of the present paper.

On that occasion only five specimens (varying in length from four to six millimetres) were obtained in a search extending over two days. These were obtained during the examination of muddy water drained from sphagnum, and were associated with *Niphargus* sp., *Neoniphargus* sp., and a small Janirid—all four of the Crustaceans being blind! An eyeless white Planarian and a delicate white Oligochæte (probably a Phreodrilid) completed the assemblage. On the second day the search was extended to the bare wet ground beyond the sphagnum-filled hollow; this had apparently once been a "button-grass"

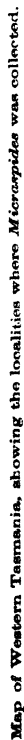
plain, but was now almost devoid of vegetation, except for scattered cushion-like clumps of a short sedge and numerous violet-flowered *Utricularias*. Across this wet patch stretched the rotting remains of a "corduroy-road," leading to Zeehan, twenty miles away, but disused for many years. The ground below these decaying logs was pitted with holes (which I believe to be those of an *Engæus*), while on the underside of the logs were seen examples of yet another blind Crustacean, this being a new species of *Phreatoicoides*. As the logs were rolled over, the phreatoicids fell, or were washed off, and wriggled swiftly out of sight in the muddied slowly-flowing water, many of them dropping down the *Engæus* burrows. Such an association is, I believe, entirely casual, as I suspect is also the case with *Hypsimetopus* (cf. Sayce, 1902, p. 218). No *Micraspides* were found in this open ground.

In the mixed assemblage obtained from the sphagnum patch, the Syncarid could be at once detected (although very similar to the two Amphipods in size and colour) by its swift gliding movement, strikingly like that of a cilia-clad organism. The legs appear outspread and doubtless are, at times, used for running and holding, but in unimpeded water the principal locomotor organs appeared to be the exopodites of peræon and pleon. To evade capture the animal would sometimes wriggle actively, and could double upon its tracks with wonderful ease and celerity.

The appended account of the animal is in the main derived from a study of the largest male (nearly 6 mm.) and the single, much smaller, female obtained at this time. Some doubts, however, as to the maturity of my specimens decided me to refrain from publication until an examination could be made of further material.

Accordingly, during the recent summer, a collecting-trip was made to Tasmania, this being rendered possible by the help of a Grant from the Council for Scientific and Industrial Research, to whom I would here express my thanks. A visit was made to the original locality, which lies by the side of a narrow-gauge ore line running from Queenstown to the power station below Lake Margaret, and is situated at an altitude of something less than a thousand feet on one of the spurs of Mt. Lyell. On this occasion collecting was poor, and one specimen only of *Micraspides* was secured. A trip to Lake Margaret, situated about 1500 feet higher up on Mt. Lyell likewise yielded only a few Amphipods, but a search in the valley of the King River (along which the new main road to Hobart is now being cut) was much more profitable. In the bed of a tiny creek cutting in places an almost perpendicular path down the hill-side, from its source just below the road, were a number of fallen trees rotted almost to the consistency of cheese, and serving to hold up a chain of linked puddles. These maintained the growth of a giant *Polytrichum*, and in the rich dark brown ooze nearly a score of *Micraspides* were found.

Some days later *Micraspides* was found in yet a third locality. This was in the vicinity of the Federation Mine on Southern Mt. Heemskirk, on the slope overlooking Trial Bay, the specimens being obtained quite unexpectedly



while digging out *Engæus* in prosecution of the search for *Hypsimetopus*. *Engæus*, the "land-crab" of Tasmania and Victoria, is found at times most abundantly in the West Coast region of Tasmania, burrowing in water-logged ground, and it was due to its destructive activities in the earthworks of a mining dam that *Hypsimetopus* had come to light nearly thirty years ago. On this occasion, *Engæus* was dug out from "soaks" near Lake Cumberland (1500 feet) high up on the mountain side, in the race below the Dam, and, at a much lower level, near the ore treatment works, and, although no *Hypsimetopus* was found, other Crustacean species were well represented. In all of these spots *Phreatoicoides* sp. was sifted out from the muddy water, which filled the hole as one dug, and was accompanied by *Micraspides*, a Janirid, and at least two Amphipods, all five of the Crustaceans being without eyes as in the collection made near Queenstown.

It is worthy of note that this West Coast Region is of extreme geological age, the rocks over the greater part of the area being classed as Pre-Cambrian and Cambro-Ordovician, with smaller areas regarded as Silurian, whereas the Central Plateau would seem to be of Permian-Carboniferous or later date.

It is probable that *Micraspides* will prove to be a form widely distributed over the perennially rain-washed slopes of the Professors' Range—to be looked for in swamps or beneath the surface of the ground, wherever that is maintained sufficiently soaked by percolating water, at altitudes of 2000 feet down to 500 feet or less. Its eyeless condition and elongate rounded body must be regarded as correlated with long-continued subterranean habits. It is of interest that the nearly related *Koonunga*, with its minute eyes, is to be found in clouded waters (liable to dry out completely), where it runs on the soft bottom ooze, into which, if disturbed, it burrows very rapidly.

ANASPIDACEA

Fam. KOONUNGIDÆ Sayce, 1907.

In general appearance like *Anaspides*, having the anterior somite fused with the head, leaving only seven free thoracic somites. Eyes sessile or absent. No antennal scale. Mandible with single dentate cutting-edge and a spinose molar expansion not separated into spine-row and molar tubercle. All the thoracic appendages except the last two bear an exopodite, all but the last have at least one epipodite. The last thoracic appendage turned backwards. Pleopoda uniramous, except the first two pairs in the male. Uropoda with large protopodite and undivided exopodite forming a tail-fan with the short broad triangular telson.

Genus MICRASPIDES, gen. nov.

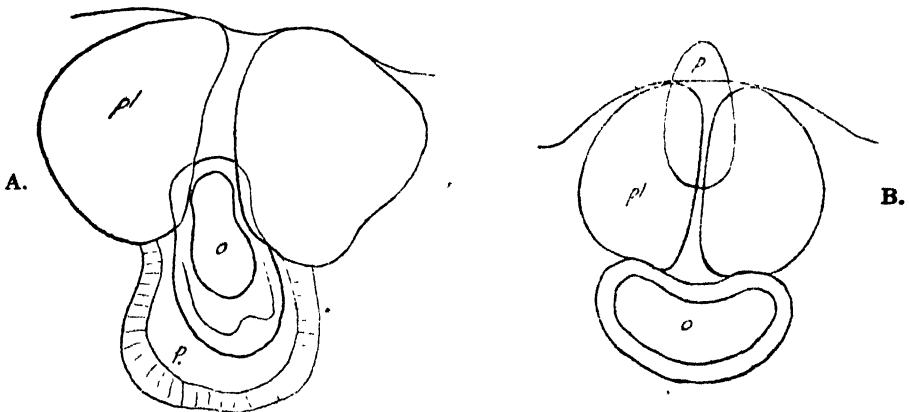
Cephalon almost equalling in length the first four (in specimens not quite mature, the first five) pereon segments: pereon short, slightly compressed, pleon-telson longer than cephalon and pereon together. Cephalon with short

transverse sulcus; frontal margin scarcely produced and with very slight incisure above the attachment of the second antenna. Eyes absent. First antenna without sensory modification upon basal joint of flagellum in the male. Second antenna scarcely shorter than the first. Mandible with 3-jointed palp. Maxillula with small palp. Maxilla with four lobes. First four thoracic appendages with two epipodites, the three following with but a single epipodite. Remarkably developed copulatory appendage on first pleopod of the male.

Remarks.—In many of its characters *Micraspides* comes very near to *Koonunga*, but the striking difference in the proportions of the peræon-segments, the absence of the characteristic antennal sensory organ in the male, the loss of an epipodite from the fourth, fifth, and sixth peræopods, and the remarkable development of the copulatory apparatus on the first pleopod in the male constitute, as I believe, differences too great to be regarded as merely of specific value.

MICRASPIDES CALMANI, sp. n.

Anterior portion of body subcylindrical, slightly compressed, gradually broadening posteriorly. First five segments of peræon short, subequal, sixth and seventh progressively longer. First four peræopods subequal, fifth slightly



A. Ventral view of "spermatheca" of *Koonunga*.

B. A similar view of the same in *Micraspides*.

o., opening into pouch; p., hinder extension of pouch in *Koonunga*, forward extension (?) in *Micraspides*; pl., paired plates.

shorter, seventh longest; the two epipodites on the anterior appendages small, a single much larger epipodite on fourth, fifth, and sixth legs. The pleon distinctly longer than the combined cephalon and peræon, the segments almost cylindrical, subequal. Telson entire, subtriangular, scarcely broader than long, the rounded hinder margin furnished with long pectinate setæ and a second fringe of short spiniform setæ below; dorsally, a more widely spaced series of pectinate setæ subterminally. Uropod with peduncle two-thirds

the length of the telson, rami subequal, longer than peduncle, fringed with long plumose setæ, replaced upon the inner margin of the endopodite by a serried rank of stout curved spines, followed by three longer spines posteriorly.

Colour.—In life transparent to whitish translucent, with brown markings very variably developed upon the dorsal surface and the bases of appendages. In the young this marbling may be practically absent, while in mature specimens the gonads—varying in colour from yellow to orange—give to the animal a tint varying from yellow-brown to red-brown. In preserved material the brown marking shows up strongly on the generally creamy-white body.

Length.—Largest specimen, a male, nearly 8 mm. ; females slightly less.

Habitat.—In muddy water, beneath sphagnum ; in the diatom-loaded ooze of moss-grown puddles or in subterranean water of the burrows of *Engæus*, near Queenstown, Mt. Heemskirk, etc., on the west coast of Tasmania.

Remarks.—This species is named in compliment to Dr. W. T. Calman, who has done so much to elucidate the structure and relationships of the living members of the Syncarida.

Detailed Description and Comparison with Allied Forms.—The general covering of the body seems to be a very tough and flexible chitin, apparently little, if at all, calcified. Intersegmental boundaries are thus not readily defined, nor could the inferior margins of the terga always be made out. The description here given is based upon complete dissections of two males about 7.5 mm. and 5.5 mm. in length, respectively, and of a female of about 7 mm.

Although, in general, it comes very near indeed to *Koonunga*, in certain particulars it approaches the condition of the Anaspididæ, while in the reduction of the epipodites, reduced size, and eyeless state, it helps to bridge the gap between the Australian surface-living forms and the minute subterranean Bathynellidæ. In the condition of the first pleopod of the male it seems to stand alone.

The *body* (Pl. 31. fig. 1) is slender (the greatest width being little more than one-seventh of the length), of almost uniform width, but widening very slightly in the pleon. In *Koonunga* there is said to be a slightly depressed condition anteriorly, whereas in *Micraspides* the body is just a little compressed in that region. In both genera the hinder part of the body is subcylindrical.

More noticeable is the difference in the size of the segments, for, in *Koonunga*, Sayce describes the segments as subequal and the cephalon-peræon as practically equal to the pleon-telson (Sayce, 1908, p. 4, pl. i, fig. 1), while in *Micraspides* the peræon is notably short, even more so than in *Anaspides* or *Paranaspides*. It resembles *Koonunga*, however, in that the number of free peræon-segments is reduced to seven.

The *cephalon*, as seen in dorsal view, appears subquadrate, produced anteriorly into a broad triangular projection much as is seen in *Koonunga*, but the incisure of the anterior margin is barely indicated in *Micraspides*, nor are there any traces of eyes. Only with difficulty, too, can the transverse sulcus be made out upon the side of the head. In the specimen figured (the smaller male)

there appeared to be a groove occupying the position indicated (Pl. 31. fig. 1), but this is not readily made out in preserved material, although it was noticed in several of the living specimens.

Except, then, for the fact that this first thoracic segment is merged, completely, in the head, *Micraspides* agrees rather with the Anaspididæ, in that the peraon-segments are not long and subequal, but are shorter anteriorly and lengthen posteriorly, only the last approaching the pleon-segments in length.

In the female, a structure (see text-fig., p. 476) comparable to that recognized by Sayce in *Koonunga* as a spermatheca, is found upon the last thoracic sternite, its crescentic or reniform opening lying well forward of the bases of the last pair of peræopods. Ventrally the pouch is almost closed by a pair of plates, but seems to encroach in the middle line upon the preceding somite. I cannot find that Sayce has figured this structure for *Koonunga*, but in a preparation which I made I fail to find the third plate he describes—on the contrary, I find two plates practically indistinguishable from the pair seen in *Micraspides*, but the ventral opening is a long oval in shape and the hinder wall of the pouch seems to lie well posterior to the plates. Probably this difference in shape and position is related to the considerable difference which exists in the size and structure of the copulatory apparatus in the two genera.

The pleon-telson region attains to a length almost twice that of the peraon, with the pleon-segments subequal; the telson is, relatively, a little shorter than in *Koonunga*; in the Anaspididæ it is still longer and narrower.

Appendages.—The *antennule* (Pl. 31. fig. 2) is approximately two-fifths of the length of the body. Its stout three-jointed peduncle is but three-fourths of the length of the cephalon, and in many cases does not show very clearly that flexure which is stated by Geoffrey Smith to occur between the second and third joints in all Syncarida. In *Bathynella* it would appear that such flexure has entirely vanished.

Upon the basal joint an oval region seemed, in my smaller specimen, to indicate the position of the statocyst; the position and shape of the opening I have been unable to make out. The outer flagellum is slender, with from 15–22 joints, and is little more than twice the length of the peduncle; the inner flagellum, 5–8 joints, is almost as long as the peduncle. Of sexual modification of this appendage in the male, such as is found in *Koonunga*, I could find no trace; sensory setæ, however, similar to those figured by Thomson (1894, p. 288, pl. xiv, fig. 4) for *Anaspides*, occur on many of the joints.

The *antenna* (Pl. 31. fig. 2) is uniramous, and is a much more slender appendage than the antennule, and it may have from three-quarters to four-fifths of its length. It resembles the corresponding appendage of *Koonunga* in the entire absence of a scale-like exopodite; the flagellum is 10-jointed.

The *upper lip* (Pl. 31. fig. 3) is rounded, its tip slightly emarginated, with a lateral setal fringe.

The *mandibles* of *Micraspides* seem to resemble quite closely those of *Koonunga*. The *palp* (Pl. 31. fig. 4) is 3-jointed, bears a few feebly-plumose

setæ, and the short terminal joint has a tuft of long setæ, both simple and plumose. The dentate edge (Pl. 31. fig. 4 a) is strongly curved, has two longer and four shorter teeth, so arranged that, in focussing, the shorter teeth appear to belong to an inner series, much as Sayce has figured for *Koonunga*.

Mesial to the cutting-edge is a structure, concerning the homology of which opposing views have been put forward by Sayce and Geoffrey Smith, the former regarding the lobe as an imperfect molar tubercle, and the spine-row is stated to be absent. Smith held that the lobe corresponded to the spine-row of other Syncarida, and believed that it was the molar tubercle which was lacking in *Koonunga*. In general appearance it certainly resembles, in *Micraspides*, a molar tubercle rather than a spine-row, but it possibly represents the two structures not separated or become confluent.

The *lower lip* (Pl. 31. fig. 5) shows the two halves almost separated in the middle line, the slight mesial expansion, seen in Sayce's figure (1908, pl. i, fig. 9) of this structure in *Koonunga*, at the junction of the lobes, is here produced into a small pointed inner lobe. The outer lobe bears a close-set fringe of longish curved setæ, and, in general, the structure resembles that of *Anaspides* rather than *Koonunga*.

Maxillula.—This appendage (Pl. 31. fig. 6) in *Micraspides* is very delicate; the proximal endite bears apically four short, sparsely feathered setæ and mesially two others, much stouter (almost brush-like) and cilia-clothed. Externally is a small plate (the pseudexopod of Hansen's terminology) and mesially a delicate proximal plate without setæ. Of this latter I can find no homologue, and at first I judged it an artifact due to displacement of tissue during dissection, but it appears in both members in both male and female dissected, and is presumably a constant feature. The pseudexopod is seen in but one appendage (where the inner endite had been mesially displaced), but it is so delicate and transparent that it is not surprising that it is not to be made out in undisturbed preparations.

The distal endite is truncated, set with ten to twelve curved spines, the innermost and one other being very slight and transparent, the two outermost simple, strongest, and longer than the rest, which are stout, subequal, and have the inner concave border finely pectinate. The small one-jointed palp bears, apically, three long plumose setæ, and points distally, but is set at a greater angle to the axis of the limb than appears, from Sayce's figure (1908, pl. i, fig. 12), to be the case in *Koonunga*. Geoffrey Smith, who has figured this appendage (1909, text-fig. 14, p. 508) represents a condition more closely resembling that of *Micraspides* so far as the palp is concerned, but his representation of the setæ arming the endites differs from Sayce's descriptions, that I can but suppose that in this Smith's specimen was abnormal.

The *maxilla* (Pl. 31. fig. 7), except for differences in the number of setæ, agrees quite closely with Sayce's figure of this appendage in *Koonunga*. There appears, however, to be some confusion in the accounts of this appendage in the Syncarida. In Thomson's account of *Anaspides*, the appendage is

described as having four branches, of which the innermost is stated to be expanded outwardly into a thin rounded lamella partly covering the next branch. Calman, in his redescription of *Anaspides* (1896), likewise recognizes four branches only, and Sayce says simply "four lobes" similar to those of *Koonunga* (1908, p. 12). Geoffrey Smith, however, figured (1909) the appendage for the three then-known Australian Syncarids, and states that "it has a very uniform structure in the three genera" (1909, p. 511). For all three he indicates five branches, to which he refers as "four endites and a palp." It must be supposed that his figure of the condition in *Koonunga* was drawn from his own preparations, for it differs essentially from Sayce's account and figure (1908, pl. ii, fig. 13), the latter author recognizing a palp and three endites only. In my preparation of this appendage in *Koonunga* I find a condition conforming exactly to Sayce's figure, *i. e.*, showing but four lobes, according to Hansen (1925, p. 101) to be interpreted as the deeply cleft endites of segments 2 and 3.

Upon the outer side of the distal lobe there is, in *Koonunga*, a single feathered seta borne proximally to the truncate mesially-directed apex; in *Micraspides* a more conspicuous seta is present, arising even more proximally. Whether or no this may be a last vestige of a palp is a question not readily decided. It certainly has no related muscle, nor even a trace of suture at its base, but it seems too remote from the apex to be regarded as merely a displaced portion of the terminal armature of this lobe.

*The First Thoracic Appendage (Maxilliped).—*This appendage (Pl. 31. fig. 8) has a close resemblance to that of *Koonunga*, but is, perhaps, somewhat stouter, relatively, and, except terminally, is much less setose. Its segments, too, are more nearly subequal, the antepenultimate and the terminal segments only being short. As in *Koonunga*, the basis has become completely confluent with the succeeding pre-ischium, so that the knee-joint is seen between what appear as fourth and fifth joints. The narrow lamellar exopodite is segmented off from the limb, and arises much more obviously from the basipoditic region of the fused segments. From the outer surface of the coxa the two small epipodites spring close together; from its inner border a narrow subtriangular lobe arises, its apex, distally directed, bearing two stout setæ, recalling those upon the inner endite of the maxillula.

In *Koonunga*, as Sayce has noted, the proximal segments of the maxilliped are flattened mesially, and upon the coxa the flattened border extends distally into a similar triangular process. Of this he remarked that had it been borne by the next distal segment it might justifiably have been regarded as the homologue of the masticatory plate of the Amphipod maxilliped. It seems reasonable, however, to consider that, both in *Koonunga* and in *Micraspides*, it is the homologue of one (or the confluence of all) of the gnathobasic lobes of *Anaspides* and *Paranaspides*. In *Micraspides* I do not find any expansion of the inner border of the basis, but in this and the four succeeding appendages the proximal rounded curve of the basis is closely set with fine short spinules, giving to this region a rasp-like surface (Pl. 32. fig. 9).

The terminal joint of the maxilliped is but indistinctly marked off from the penultimate, and bears one large and three slightly smaller curved movable spines (the enlarged setæ of Smith's descriptions) surrounded by a brush of delicate recurved setæ.

Peræopods (*Thoracic appendages* 2-8).—These are all more slender than the maxillipedes, but otherwise generally similar in the arrangement and proportions of the segments (Pl. 32. figs. 10, 11). The eighth, as in *Koonunga*, is flexed in the opposite direction to the rest, the dactyl being directed forwardly.

In the relative length of these limbs, *Koonunga* appears to differ from *Anaspides*, and *Micraspides* from both. Thomson describes the second, third, and fourth legs of *Anaspides* as becoming progressively longer, the fourth being the longest; the fifth is said to be slightly shorter, the sixth, seventh, and eighth progressively shorter, in the last the diminution being described as most pronounced. In *Koonunga* it is the fifth thoracic appendage (fourth peræopod) that is longest, the second, third, fourth, sixth, and seventh being shorter and subequal, the eighth slightly longer, but less than the fifth. But in *Micraspides* it is the sixth thoracic appendage which is shortest, the second, third, fourth, and fifth being subequal and rather longer, the seventh and eighth still longer, the last being quite the longest. I am not certain, however, whether these are constant in the adult: in the immature specimen first examined, these measurements were different, the fifth of that animal being the shortest, although the last was again the longest. The maxilliped seems permanently flexed, but if straightened out would be, at least, as long as any of the four succeeding limbs.

Upon all but the last of the peræopods there is present on the coxa, in both sexes, a mesial lobe (Pl. 32. figs. 9, 10, 11) comparable to that described above as the gnathobasic lobe of the maxilliped. In the female these undergo a slight enlargement on fifth and sixth peræopods into more rounded fringed lobes. In *Koonunga* these two lobes of the female appear to be the only remnants of the series, but in *Anaspides* it would seem from Thomson's description (1894, p. 290) that they persist upon some, at least, of the legs in the male, as well as being developed upon the fourth, fifth, and sixth peræopods of the female.

The *exopodites* in *Micraspides* are stouter and slightly longer, relatively, upon the more posterior limbs, almost equalling the endopodite in the case of the fifth appendage in my smaller specimen. In the fully grown specimen it nowhere exceeds two-thirds of the length of the endopodite. Concerning the function of these rami, Smith remarks (1909, p. 471) that in *Paranaspides* they appear to be always waving and are, presumably, respiratory. In *Micraspides*, as stated above, they are important locomotor organs, the movement of the animal seeming to be effected normally by swimming rather than running, the legs carried outspread. The gills, too, are capable of independent movement, so that they can be waved while the animal is stationary.

As in all the extant Syncarids (excepting the Bathynellidæ) the exopodites borne on second to sixth thoracic legs are multisegmented, but in *Micraspides* there are rather fewer segments than in *Koonunga*. Of the latter Sayce states that there are "about seven," but in the by no means large specimen which I dissected there were as many as nine. In *Micraspides* the number is six or seven (counting the large peduncular joint), eight being found in but a single limb. In my immature specimen the number nowhere exceeded six.

In *Micraspides*, as in *Koonunga*, the seventh leg is without an exopodite; in the Anaspididæ the ramus, though present, is reduced to an unsegmented lamella like that seen in all Syncarida upon the maxilliped. In *Bathynella*, according to Chappuis (1927, p. 599), all of the seven thoracic exopodites are simple one-jointed lamellæ, while in *Parabathynella* those which persist have retained two joints.

Epipodites.—The arrangement and number of the epipodites in *Micraspides* also show a condition intermediate between that of the other Australian Syncarida and the Bathynellidæ. Upon the maxilliped and the three succeeding peræopods there are two epipodites (Pl. 31. fig. 8; Pl. 32. fig. 10), which differ from those of *Anaspides* and resemble those of *Koonunga* in being small and unequal. They are set close together upon the outer aspect of the coxa, from which they are segmented off by a distinct suture, presenting the appearance of a short peduncle widening distally and a long oval lamella, the more distal gill being the larger member of the couple. Upon the three succeeding legs of both *Anaspides* and *Koonunga* these two branchiæ persist, but those upon the last gill-bearing limb are markedly reduced in size. In *Micraspides* only one is retained (Pl. 32. fig. 11), this corresponding to the more distal member, but it is enlarged and appears as a broad rounded oval plate.

This reduction in the number of epipodites is still more evident in *Parabathynella*, in which no limb bears more than a single gill.

In the *pleon* all of the segments bear appendages consisting, in the first five, of a flagelliform exopodite (Pl. 32. fig. 14) in general resembling those borne upon the thoracic appendages and having approximately the same size and about as many segments. Upon the peræopods, however, the first joint of the exopodite appears as a stout basal portion (the "peduncular joint" of Sayce's and Thomson's descriptions) springing directly from the basis. In the pleopods this peduncle appears to be inserted into the sympodite, but to have a minute intercalated joint set in obliquely at the junction. Under a high magnification this structure appears rather as a minute lamelliform scale (Pl. 32. figs. 13, 14) external to the base of the peduncular joint, and is difficult of explanation. It is to be made out on all of the pleopods of the female and upon at least the four hindmost of the male. In the limb figured (Pl. 32. fig. 14) it seems to rise from the mid-region of the sympodite and may perhaps be a vestigial epipodite.

In the male the endopodite persists upon first and second pleopods, in which it is modified to form part of an elaborate copulatory apparatus. In the first pleopod (Pl. 32. fig. 12) this arises from a short broad sympodite, to the inner

aspect of which it is attached by a narrow jointed (?) stalk. Distally it swells into a subglobose mass divided into inner and outer halves. Both appear to be hollow, the inner gaping widely below, the lip slightly reflected and bearing a flattened cone or rosette-like cluster (Pl. 32. fig. 12 *b*) of hooked spines, from which a single larger hook may stand detached. The outer piece is still more widely open distally, with its lip produced into a number of serrations or flattened spines. Just within the lip is a powerful spine, whose appearance suggests that it may be extrusible (Pl. 32. fig. 12 *b*). Between the two masses, but apparently derived from the outer, is a third (smaller) lobe crowned with a dense tuft of curled hook-like setæ.

This structure, while undoubtedly the homologue of the more nearly cylindrical piece of other Syncarida, seems to have reached a complexity seen elsewhere in the Malacostraca only, as Dr. Calman has reminded me, in the Euphausiacea, and the Penicidae. It is, of course, possible that the organ figured by Sayce in *Koonunga* was not fully developed, but that structure does agree fairly well with the comparable organ in *Anaspides*. In the somewhat smaller specimens of *Micraspides*, obtained in 1927, the structure appears more simple, as a concave plate divided distally into two lobes, one of which is again subdivided, and there are no hooks.

Upon the second pleopod of the male (Pl. 32 fig. 13) the endopodite is less noticeably different from that of other Syncarida - indeed, except in its proportions, it differs little from that of *Koonunga*. It arises from the sympodite by a narrow stalk, swells to a rounded cylindrical piece, which bears mesially, near its distal end, a close-set cluster of short hooks (Pl. 32. fig. 13 *a*), thirty or more in number, which presumably act as coupling-hooks. This is followed by a terminal piece, concave externally, and narrowing to an incurved tridentate point, directed laterally, the denticles being dark yellow-brown in colour and strongly chitinized. Undisturbed, the pair lie closely apposed in the middle line and extend forwardly between the bases of the first pair of copulatory organs. In the smaller male examined the organ is much less completely developed, and shows no sign of the lateral cluster of hooks.

In *Micraspides* I find no trace of the median sternal process described by Sayce as so conspicuous in *Koonunga*. It is noteworthy that, although it is likewise unrecorded for *Anaspides*, in *Paranaspides* Smith has figured (1909, text-fig. 29, p. 520) what may perhaps be a vestige of this structure.

The *uropodu* bear a very close resemblance to those of *Koonunga*. The peduncle is, relatively, slightly longer and almost devoid of spines. The rami are almost equal and armed with spines and setæ, as in *Koonunga*, but those upon the inner border of the endopodite are sharply curved and appear denticulate.

The telson (Pl. 32. fig. 15) is very slightly broader than long, its base protected by three pairs of strong spines, which arise from the hinder margin of the sixth pleon-segment. The posterior border has a close-set fringe of stout pectinate spiniform setæ, immediately ventral to which, and visible only by deep focussing,

another shorter fringe of spines, some pectinate and others remarkably barbed. Dorsally and submarginally is a series of more widely spaced, strong, pectinate setae.

ADDENDUM.

The outstanding characteristic of the work of that veteran carcinologist, the late G. O. Sars, has always been the beauty and accuracy of his figures. It is peculiarly unfortunate, therefore, that in his last published paper * an error should have crept into his drawing of *Parabathynella malaya* (pl. vii, fig. 2), in which the animal is represented as having but *five* instead of *six* pleon-segments. That it is a mistake will be evident from a comparison with his text and with his other figures of the entire animal (pl. vii, fig. 1 and pl. viii, fig. 1). The matter has, moreover, a certain importance, since it minimises the length of the pleon and may have led to Sars's statement (p. 340) that the middle region of the body is "by far the longest," whereas it actually is little longer than the pleon.

Much more serious, however, is the fact which emerges from a reading of his discussion of the relationships of *Parabathynella* (in the course of which he states that the affinities of the Bathynellidæ with the Anaspidacea are extremely remote), for it becomes evident that Sars had not fully acquainted himself with the literature on the Syncarida. He refers briefly to Calman's 'Crustacea' (1909) as containing a "supposition that *Bathynella* might be a degenerate member of the Syncarida," and completely overlooks more recent works by the same author (1911 and 1917). In the latter of these, Calman had added much to our knowledge of *Bathynella*, entering very fully into the question of its relationships and completely establishing its position as a Syncaridan.

Advocating the removal of the Bathynellacea from the Syncarida, Sars suggests the establishment of a new Malacostracan order which should include the Bathynellacea united with a second suborder, the Thermosbaenacea (the latter containing Monod's new species *Thermosbaena mirabilis* †), the order being regarded as an assemblage of extremely primitive forms, directly ancestral to other living Malacostraca—more particularly the Amphipoda and Isopoda. Such a proposal is to be regarded as a consequence of Sars's failure to rid himself of the idea that the Amphipoda and Isopoda are "lower" forms than those which exhibit the "caridoid" facies, notwithstanding that this view has been completely discredited by the work of Claus, Boas, Hansen, and Calman.

Even so, it is difficult to discover upon what grounds Sars would associate *Thermosbaena* (which is an undoubted Peracaridan) with the Bathynellacea. On the other hand, these, notwithstanding their distinctive peculiarities, have very much in common with the Australian Syncarids, the most recently discovered of the latter serving in many ways to link them still more closely.

* 'Journal of the Federated Malay States Museums,' vol. xiv, pp. 339-351, pls. vii & viii.

† Erroneously attributed to Seurat.

Thus, in the living Anaspidacea we find an interesting series :—*Paranaspidæ*, still retaining the free swimming habit and *Mysis*-like conformation and primitive condition of the mouth-parts, is found living only in the open waters of a vast lake, which has probably persisted from Permo-Carboniferous times. *Anaspidæ*, restricted to smaller bodies of water on the fringe of the Central Plateau, and prone to retire into crevices, its body flattened to a semi-cylindrical shape and quite obviously adapted to a running or creeping habit (though still capable of swimming and of using its tail-fan for sudden movement, the uropods having retained broad lamellar rami). In both of these the eyes are stalked, the antennules, antennæ, peræopods (except the last), and the pleopods biramous, the peræon-appendages having, in addition, each a couple of respiratory lamellæ (epipodites). In the pleon-appendages, one ramus (the endopodite) has become one-jointed and lamellar, and, as a frequently occurring individual variation, there is a tendency towards degeneration, one or more of the hindmost pleopods becoming uniramous.

Koonunga is to be found only in the cloudy water of small water-holes, dams, etc., which are liable to complete drying out. The animal is still capable of swimming, but for the most part moves by creeping over the fine clay mud of the bottom, into which it can burrow with remarkable celerity. As compared with the Anaspididæ, it is greatly reduced in size, its body is more nearly cylindrical and the free segments subequal, the eyes small and sessile, the second antennæ without exopoditic scale. The thoracic epipodites, too, are undergoing modification, being no longer large and subequal, but unequally reduced in size. The peræopods, though their number is undiminished, are without exopodites on the two hindmost.

Micraspidæ has apparently undergone still further degeneration. The animal is, as stated above, to be found leading a wholly cryptozoic life in the muddy floor of shallow swamps, beneath sphagnum, or in the water or liquid mud which fills the burrows of the "land-crab" *Engæus*. Transferred to clear water it swims easily, but can also move by a wriggling of the flexible, almost vermiform, body. It is still further reduced in size, and is eyeless, practically colourless, and almost transparent. Its antennæ are relatively shorter and simpler, the epipodites are reduced in number, only one lamella being present on the fifth, sixth, and seventh thoracic limbs. The exopodites are shorter and have fewer joints than the corresponding structures in *Koonunga*.

In both *Koonunga* and *Micraspidæ* the mouth-parts have undergone a distinct degradation (as compared with those of *Anaspidæ* and *Paranaspidæ*), the mandibles having a triturating process no longer divisible into spine-row and molar, the maxillæ showing considerable simplification. The maxillipedes differ little from the following thoracic appendages, except in being stouter, in having developed a permanent flexure, and in that they are perhaps slightly more setose.

From the condition exhibited by these two members of the Koonungidæ, that of the Bathynellidæ differs only in degree. Life in wholly subterranean

waters enduring over a vast period of time would suffice to explain the further reduction in size, the complete blindness, and transparency. The uniformity of the segmentation has a close parallel in *Koonunga* *, the simplification of the thoracic limbs merely marks a further stage in the reduction of the number of joints, a tendency to which is clearly shown in the Anaspidacea : the reduction in the number of epipodites has actually gone further in *Micraspides* than in *Bathynella*, though not so far as in *Parabathynella*. An accompanying simplification of the mouth-parts is rather to be expected with the decrease in the size of the animal and of the limbs generally : the change in the mandible has gone little farther than in the Koonungidae, in which group the loss of the exopoditic scale from the antenna has likewise occurred, while within the Bathynellidae themselves there is evidence of degenerative changes leading to the loss of the inner flagellum of the antennule.

The gonads and reproductive apparatus are restricted to the pleon in *Micraspides* (probably in *Koonunga* too), in this agreeing strictly with the Bathynellidae.

The only remaining differences to which Sars has directed attention are (1) the absence of pleopoda, (2) the presence of a copulatory organ in the male upon the eighth thoracic segment, and (3) the presence terminally of a paired structure, which Sars has interpreted as a pair of telsonic uropoda.

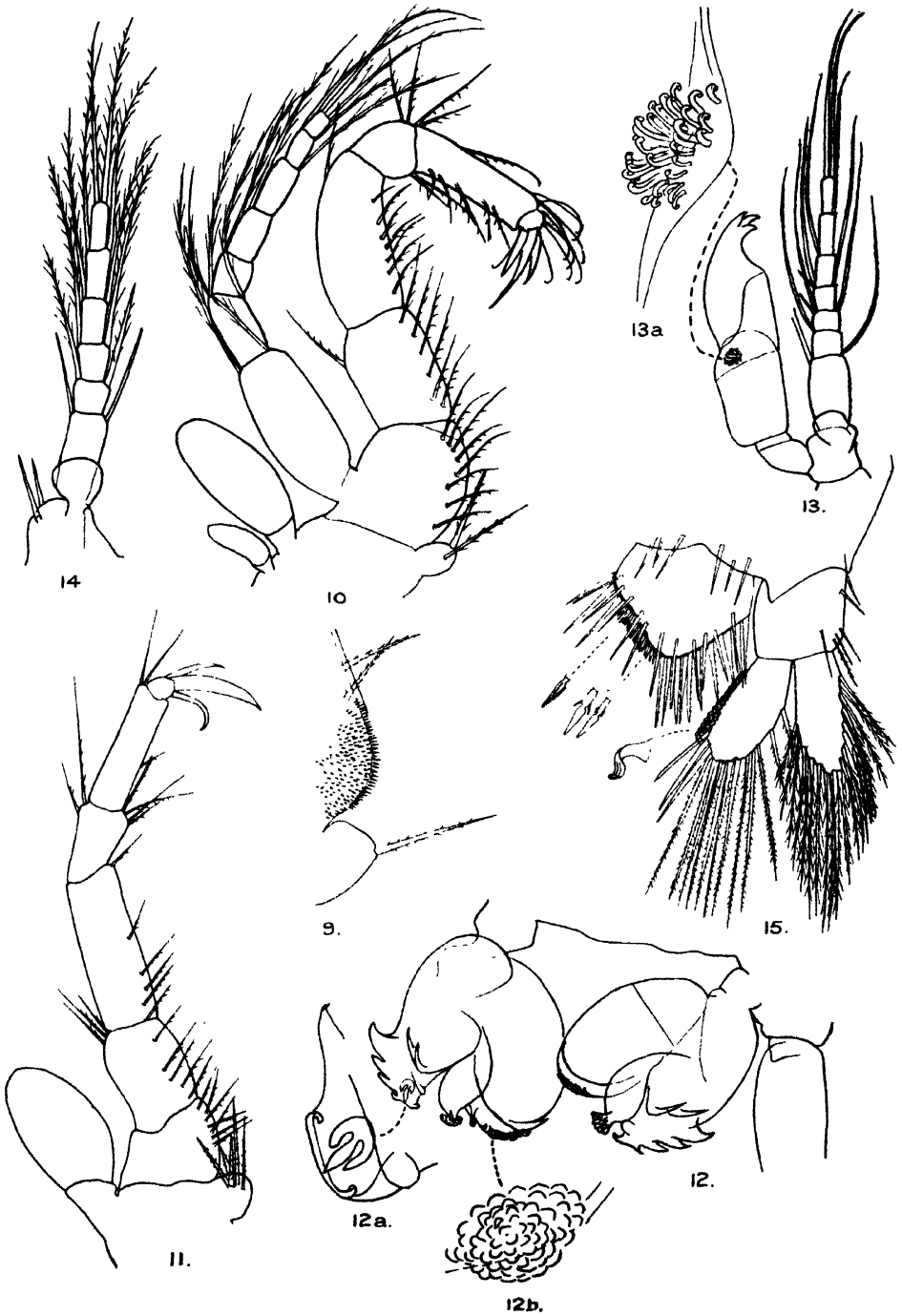
The loss of more or fewer pleopods is, however, of no great importance, and occurs in many Crustacean groups ; as pointed out above, there is a definite tendency in *Anaspides* to reduction here, one ramus frequently being wanting on the hindmost pleopoda, while in *Bathynella* the first pair are retained. In any case, it is scarcely probable that this absence of pleopoda could have been a *primitive* Malacostracan feature.

The "copulatory organ" on the eighth thoracic segment is clearly different in character from the modified pleopods of the first and second pairs, to which the name is applied in various other orders of Malacostraca. It appears to be perforated by the vas deferens, of which it represents the prolapsed or exerted terminal portion. In the Isopoda and Amphipoda such an exerted tubular structure extending the vas deferens is found on the last thoracic segment, and in the Phreatoicidae, at least, it is definitely related to the coxa of the appendage. In the latter group, however, this structure is occasionally found in female as well as in male specimens—a condition which suggests that we may be dealing with an appendicular structure which has been modified for sexual purposes.

* The freedom of the *first* thoracic segment is a unique feature, but may have been a re-acquirement of freedom by a segment in which fusion with the head had already begun. It is of interest that in a parallel group—the Phreatoicidae—the surface-forms have lost the freedom of the *second* thoracic segment, but in the subterranean genera this segment is invariably found free, and may actually be as long as, or longer than, the succeeding segments, notwithstanding that in other particulars the subterranean forms have undergone degenerative changes (loss of eyes, epipodites, etc.).



MICRASPIDES CALMANI, sp. nov.



MICRASPIDES CALMANI, sp. nov.

As regards the paired terminal structures, interpreted by Sars as a second pair of uropods, but which Chappuis has suggested may represent the paired halves of a cleft telson, a suggestion with which Calman is in agreement, it may be pointed out that their occurrence lends no support to the suggested Amphipodan relationship, unless it be supposed that some of the more anterior pleon-segments are lost in the Amphipoda, for in the Bathynellidae the undoubted uropods are borne upon the sixth pleon-segment and, therefore, may be regarded as homologous with the *third* pair of Amphipodan uropods.

That these terminal structures are really the halves of a cleft telson appears much more probable, the fact of their mobility in no way militating against this. In the Gammaridea the telson is found in every state from an undivided lobe to a completely cleft and freely movable paired structure. In the Phreatoicidea, too, we find a telson which varies from the long spine-like condition seen in *P. tasmaniae* to a transversely projecting or upturned ledge as in *P. australis*, emarginate in *Amphisopus lintoni*, and actually deeply cleft in *A. latipes*.

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DESCRIPTION OF THE PLATES.

PLATE 31.

- Fig. 1. Male of less than 6 mm. in side view.
2. Antennule and antenna of larger male.
3. Upper lip of the same.
4. Mandible of the same.
- 4 a. Dentate edge and "molar" of another specimen, more highly magnified.
5. Lower lip of larger male.
6. Maxillula of the same.
7. Maxilla of the same.
8. Maxilliped of the smaller male.

PLATE 32.

- Fig. 9. Coxal lobe and portion of basis, showing rasp-like surface.
10. Third peræopod of larger male.
11. Sixth peræopod of the same.
12. Endopodites of first pair of pleopods of large male.
13. Second pleopod of the same.
14. Fifth pleopod of the same.
15. Telson and uropod of small male ; terminal setæ on telson shown on one side only,
to expose deeper barbed spines.

Further Observations on Biological Races in *Hyponomeuta padella* (L.). By
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(Communicated by Professor J. STANLEY GARDINER, F.R.S.)

[Read 9th January, 1930.]

DURING the writer's absence in the United States the genetical work on different biological races of *H. padella*, which it was hoped it would be possible to carry on, came to an end, owing to the death of all the hibernating larvæ. The reason for this failure is not altogether certain, although there is little doubt that it was in part due to the severe winter temperatures (1927-28). A decrease in the field-infestations of both *cognatella* and *padella* in the Cambridge district, particularly near St. Ives (Hunts), was very noticeable, and it seems quite reasonable to suppose that an insect that winters as a larva would be more easily endangered in this way than one which passes the winter as an egg.

Although the most interesting part of the work has had thus for the time being to be abandoned, the discovery of a very big infestation of *padella* on Blackthorn near Rye, Sussex, made it possible to obtain further data on certain points which had not previously been studied as fully as was desirable.

In the previous paper evidence was brought forward which pointed to the existence of a subsidiary biological race on Blackthorn (*Prunus spinosa*), differing in host-plant preferences from the hawthorn form. The difference between the two was quite clearly very much slighter than that between the hawthorn and apple form; but the experiments, while suggestive, were not on a large enough scale to be conclusive. The work carried out this summer (1929) was designed to throw more light on this particular matter. Although incomplete in some respects it has been thought best to publish these notes, as it is doubtful whether the writer will be in a position to pursue the matter any further for the present.

As in previous experiments, the insects were taken from Blackthorn as fully fed larvæ or as pupæ. On emergence they were placed in large cages in the insectary and given a choice of food-plants for egg-laying. The cut sprays of food-plant were removed at intervals throughout each experiment, and a record kept of the number of eggs laid on each species of plant. Great care was taken to ensure that the results should be significant. Thus the relative position of the different plants in the cage was altered from time to time, so that preference for a particular part of the cage, due to differences of lighting or temperature, should not vitiate the result. Since it is impossible to be certain that one has put in exactly equal proportions of the plants, or, in other words, supplied exactly equal egg-laying facilities, care was taken that the kind of food-plant from which the form experimented with had been reared should always be present in, if anything, slightly less quantity than the other.

The figures given are thus, if anything, an under-estimation of the strength of the host-preference.

Table I. requires little comment. In all these experiments there were never any instances of eggs being laid on the glass or woodwork of the cages.

As was recorded in the previous paper, moths of the Apple form could not be induced to lay eggs on Cherry, although there are records of this plant being extensively attacked under natural conditions.

TABLE I.

H. padella. Moths reared from Blackthorn (*P. spinosa*) and given choice of Blackthorn and Hawthorn for oviposition.

Experiment.	Total no. of egg-masses.	Total no. of eggs.	On Blackthorn.		On Hawthorn.	
			Masses.	Eggs.	Masses.	Eggs.
1	11	400	6	238	5	162
2	4	109	3	73	1	36
3	17	608	8	306	9	302
4	7	169	4	88	3	81
5	20	725	17	641	3	84
6	26	679	25	644	1	35
7	9	373	7	334	2	39
Totals	94	3063	70	2324	24	739

TABLE II.

H. padella. Moths reared from Blackthorn and given choice of Blackthorn, Hawthorn, and Cherry for oviposition.

Experiment.	Total no. of egg-masses.	Total no. of eggs.	On Blackthorn.		On Hawthorn.		On Cherry.	
			Masses.	Eggs.	Masses.	Eggs.	Masses.	Eggs.
1	8	366	3	170	5	196	0	0
2	8	314	5	174	3	140	0	0
Totals	16	680	8	344	8	336	0	0

Table II. gives the results of a similar inquiry carried out with the Blackthorn-reared moths. No oviposition on Cherry could be obtained.

Taking the figures from the two tables it will be seen that out of a total of 110 egg-masses containing 3743 eggs, 71 per cent. were laid on the original food-plant *P. spinosa* and 29 per cent. on Hawthorn.

Although the average size of the egg-masses on Blackthorn is larger than on Hawthorn, the difference, 34.2 as against 33.5, is so small as to be negligible. This is in marked contrast to the results of an experiment recorded previously, in which the figures were 45.7 and 28.5, respectively.

It will be seen that these experiments have indicated a stronger preference for Blackthorn than was to have been expected from previous work, which, although on a smaller scale, gave 58.4 per cent. on this plant and 41.6 per cent. on Hawthorn. There seems, however, to be a very plausible reason for this.

The moths in the earlier experiment were obtained from a field in Huntingdonshire, where both food-plants were present in close proximity to each other. Since, under such conditions, a certain amount of food-plant change undoubtedly takes place, it is improbable that the strain employed had been isolated on Blackthorn either very completely or over any very long period.

The moths employed in the other case were collected as full-fed larvæ or as pupæ from a large isolated patch of stunted Blackthorn bushes growing on the shingle of Dungeness beach, Sussex. So far as is known, there were no Hawthorn bushes present within at least a mile—possibly much more; consequently it is likely that this strain had been completely isolated on its food-plant for a long period. They were present in such enormous numbers that there was hardly a leaf left anywhere on the bushes. The whole area was white with their webbing, which extended in places a foot or more over the surrounding shingle, and covered tufts of grass and other herbage. In places many of them were dying of starvation. In view of this, it is perhaps not surprising that the host-plant preference should have been more strongly implanted than in the former case.

It was hoped to obtain further data with regard to the behaviour of the Hawthorn-reared insects—previous observations having indicated a preference of a similar nature for *Crataegus*. Unfortunately, a high percentage of parasitism among the insects which were to have been used in these experiments rendered it impossible to carry them out on a large enough scale for the results to be significant.

Experiments on the mating-preferences in line with those already recorded were also undertaken between the Hawthorn and Blackthorn forms. These showed a surprisingly strong tendency for like forms to mate together. The figures were, however, discarded as unreliable. Owing to the scarcity of food, the majority of the moths from the Sussex locality were undersized, and consequently there may well have been an actual physical disability which hindered cross-mating.

The conclusion arrived at previously, after experiments on a large scale, that the long-continued breeding of *H. cognatella* on the evergreen *Euonymus japonicus* (the original food-plant being the deciduous *E. europæus*) has not so far developed any preference for that host-plant, was further borne out this

season. Moths taken as pupæ from *E. japonicus* were given three species for egg-laying in approximately equal quantity, with the following results :—

Total.		<i>E. hamiltoniana</i> (deciduous).		<i>E. americana</i> (deciduous).		<i>E. japonicus</i> (evergreen).		On woodwork of cage etc.
Masses.	Eggs.	Masses.	Eggs.	Masses.	Eggs.	Masses.	Eggs.	
18	728	6	220	9	395	3	113	None.
Average size of egg-masses.		} 37		} 44		} 37		

In respect of the tendency to form biological strains, it seems fairly clear that *H. cognatella* is in marked contrast to *H. padella* and its forms.

SUMMARY.

It has been shown previously that the small Ermine Moth, *Hyponomeuta padella* Linn. (*H. variabilis* Zell., *H. malinella* Zell.), is split into two well-marked biological races—one attached to Apple and the other to Hawthorn (*Crataegus oxyacanthi*), Blackthorn (*Prunus spinosa*), etc.

Further evidence is now brought forward which suggests that the latter form is itself split into two less strongly marked subsidiary races, one attached to Blackthorn, the other to Hawthorn.

REFERENCES.

- THORPE, W. H. 1929. Biological Races in *Hyponomeuta padella* L. Journ. Linn. Soc., Zool. xxxvi. pp. 621-634.
 —. 1930. Biological Races in Insects and Allied Groups. Biological Reviews, v. pp. 177-212.

Studies in Colour-changes in Fish.—Part V. The Colour-patterns in certain Flat-fish and their Relation to the Environment. By H. R. HEWER, M.Sc.
(Communicated by Professor E. W. MACBRIDE, F.R.S.)

(PLATES 33 & 34, and 11 Text-figures.)

[Read 15th May, 1930.]

INTRODUCTION.

In a previous paper (5) the author has given an account of the colour-patterns of *Pleuronectes limanda* (dab), and during those investigations several other species of flat-fish were examined superficially, and certain points appeared in common with the dab. This led to the conclusion that a detailed examination of other related species and genera might give interesting results not only as a basis for further observations on the power of adaptation possessed by different flat-fish, but also as giving some idea of the origin and evolution of the complicated patterns themselves.

The work of Sumner (9) and of Mast (6), among that of others, has shown fairly conclusively that the general tendency of the coloration is protective or adaptive—at any rate, under laboratory conditions. If this is also to apply to the fish in their normal environment, some degree of correlation should exist between the habitat of a species and its development of colour-patterns. This resolves itself into a simple matter of observation and recording, but certain problems arise as soon as any interpretation of results is attempted. For example, if the colour-patterns are of recent development—are, in fact, produced under the same environmental conditions as those prevailing during the stabilisation of the species,—we might expect considerable approximation to the background if our thesis is to hold good. But if, on the other hand, these patterns are of considerable age, dating back to the rise of the family or even further, then the adaptation must obviously be a compromise between the hereditary scheme of patterns and the perfect adaptational scheme which we could possibly imagine. If the latter is true the extent of the compromise is the problem to be dealt with.

Arising from this is the question of the evolution of the patterns themselves. Unless the microscopic details of the response to a changed environment in laboratory experiments are in general accord with the trend of evolutionary development of the patterns, any conclusions drawn from such experiments are useless, as in all probability an entirely different mechanism to that employed by the animal in the course of its evolution is being tested.

During the summer of 1928 specimens were obtained and preparations made to elucidate these points. The following species were used* :—*Pleuronectes platessa* (young 6–10 cms. and adults), *P. flesus* (adults), *Microstomus microcephalus* (adults), *Arnoglossus laterna* (adults), *Zeugopterus punctatus* (adults), *Rhombus maximus* (young 5–6 cms.), *R. lævis* (adults), and *Solea vulgaris*. Subsequently I obtained further data, in the case of *Psettodes* spp. from material in the British Museum, while the facts concerning *Bothus podas* and *Paralichthys albiguttus* are deduced from photographs in papers by Sumner (9) and Mast (6) respectively.

In certain cases it was possible to estimate roughly the nature of the bottom from which specimens were taken, so that points of correlation between the background and the patterns of the fish could be noted. Apart from my own observations of particular instances and also fairly general and well-known statements, there is, however, little information of any direct significance. The whole matter is further complicated by the extensive range of some species, so that many types of bottom are inhabited during a lifetime. Borley's papers (1 and 2) on the bottom of the North Sea treat the matter from a somewhat different angle, and the general effect of the bottom is difficult to visualise. Records of catch, to obtain an idea of the habitat most frequented, are often misleading owing to the fishing concentrating on certain periods of the year, so that an entirely wrong idea of the general habitat of the fish may be obtained.

My own material was dealt with by the process described in connection with the dab. It is only necessary to add that, as preparations made in the autumn of 1925 still retain their colour perfectly in the centre, I have not altered the method in any way.

I am greatly indebted to the staff at the Laboratory at Plymouth, without whose kindly assistance the collection of so much material in the short time available would have been impossible. I am also indebted to Prof. MacBride and Dr. O. M. B. Bulman for assistance and advice in the preparation of the manuscript.

THE PIGMENT CELLS.

The colour of flat-fish is due to pigment contained in cells (chromatophores) distributed in three layers in the skin. One layer is in the epidermis and two, an upper and a lower, in the dermis. The chromatophores are of three kinds :— (a) The melanophores contain a blackish-brown pigment called melanin, and may be present in any of the layers. (b) Other cells contain pigment of a variety of shades from deep red to pale yellow. Two names are applied to these : xanthophores when the pigment is yellow, and erythrophores if an orange or red pigment is present. Xanthophores may be present in the two dermal layers, and erythrophores in the upper dermal and epidermal layers. (c) The third type is the iridophore, which contains guanine and is opaque white. These

* The classification used in this paper is that of Tato Regan (1910), with the subsequent modifications that have become necessary in accordance with the laws of nomenclature.

do not "expand" and "contract" like the others, but are polygonal in shape. They occur only in the dermal layers.

The lower dermal layer seems to form a background of colour, but does not take any important part in the colour-patterns or in the colour-changes. The chromatophores of the upper dermal layer play the largest part in the formation of the colour-patterns, and these are the only ones referred to in this paper unless otherwise stated. Except in a few species, the epidermal chromatophores are few in number.

THE COLOUR-PATTERNS.

By a differential distribution of these chromatophores most of the colour-patterns are produced. On examining any flat-fish a number of spots can be seen of varying size and shape and in many cases of differing colour. Despite these differences they can be grouped together into what I have termed patterns. The well-known orange spots on the plaice may be taken as an example. These spots all agree in microscopic details, and together form a pattern. To these patterns I have given names to facilitate reference, and because I believe them to be quite definite structures in the fish.

At the risk of anticipating the results, it is convenient to state at this point that these patterns, now to be enumerated, hold good within a range of variation throughout all those species examined in detail.

The patterns fall into three groups. The first group (A) is that exhibiting a definite distribution, so that many spots of a given pattern occur in the same places in all members of a species. Spots of such patterns may, however, occur elsewhere, but not with great regularity. The second group (B) includes patterns whose distribution is quite general and irregular, and the third group (C) is defined as those for which a morphological basis in the distribution of chromatophores cannot be found, but which appear to owe their existence to the differential expansion of the chromatophores over that area. They, too, are quite definite in their distribution.

Group A consists of two patterns, the *orange and black spots* and the *white spots*.

Orange and Black Spots are typified by the very large number of erythrophores and melanophores which they contain. Epidermal melanophores may increase the dark appearance. These spots are sometimes divided into black and red parts, in which melanophores and erythrophores respectively are especially numerous. There are few iridophores on these spots.

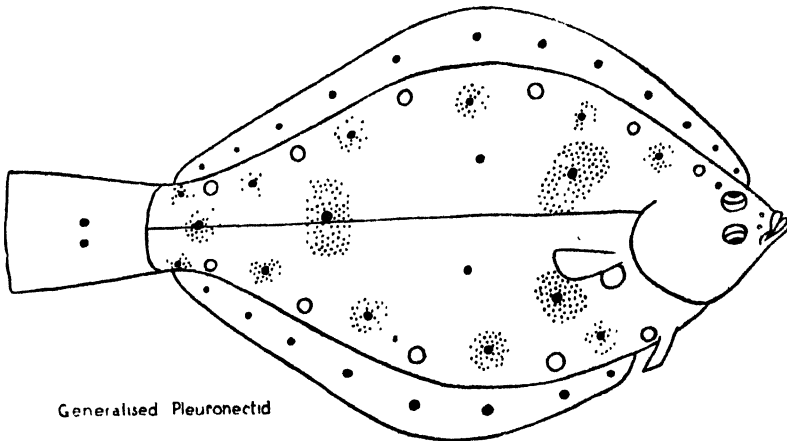
White Spots are characterised by the presence of very many iridophores, which are grouped round the melanophores. This grouping is very typical, for it is by the expansion of the melanophores that the iridophores are covered and the white spots disappear. As these spots may be seen or not according to the condition of the melanophores, they are termed "facultative." There may be erythrophores present, but there is a tendency towards their elimination.

Group B also consists of two patterns, the *pale spots* and the *normal area*.

Pale Spots are recognized by the complete absence of the erythrophores and xanthophores, the result being a greyish tinge rather than a yellow or pale brown appearance macroscopically. There is in some species a slight tendency towards grouping the iridophores round the melanophores. This is not diagnostic of the pattern, however.

The *Normal Area* is composed of the rest of the surface of the skin not modified into any of the foregoing patterns. Comparisons of numbers of chromatophores present in the other patterns are always made with this area. In most species this area is subdivided according to the presence of xanthophores or erythrophores—the former is termed the yellow phase, the latter the red phase. The yellow phase may have epidermal melanophores as well as the dermal chromatophores.

TEXT-FIG. 1.



Scheme of constant spots in the Pleuronectiformes. Orange and black spots, black; white spots, rings; dark patches, dotted.

Group C is comprised of only one pattern, the *dark patches*.

Dark Patches.—A large number of these areas have been examined in several species, and in no case could a differential distribution of chromatophores be found. Their appearance can be directly attributed to an "expansion" of the chromatophores on them as compared with the cells in the surrounding skin, and are therefore "facultative."

The distribution of the patterns in Groups A and C have already been stated to be quite definite in the case of many of the spots composing the patterns. This appears to hold good for all of the species of the Pleuronectiformes here examined. In text-fig. 1 there is drawn up a generalised scheme of these three patterns, which, while being convenient for reference, represents what I believe

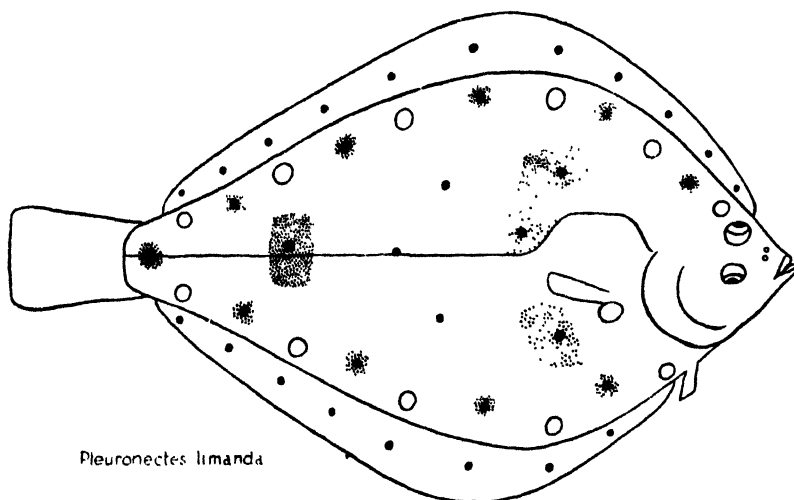
to be the common denominator of the colour-patterns found in the *Pleuronectiformes*. The patterns in Group B are not included, as they are distributed generally.

The orange and black spots are found in a line along the dorsal and anal fins, in a line along the dorsal and ventral margins of the body, and also at intervals on the lateral line. There are a few spots arranged symmetrically with regard to the lateral line in between the other lines of spots.

The white spots occur between the orange and black spots along the margin of the body. There may be others along the lateral line and even between these rows, but I am not certain enough of their constancy to include them in the generalised scheme. There is one at the base of the pectoral fin which is very constant throughout.

The dark patches are always associated with orange and black spots, as I have shown in the figure. They are on the whole remarkably constant through the forms studied, with the exception of *Psettodes*.

TEXT-FIG. 2.



Scheme of constant spots in *Pleuronectes limanda*. Orange and black spots, black; white spots, rings; dark patches, dotted.

DESCRIPTION OF SPECIES.

In the *Pleuronectidæ* four species have been examined :—

PLEURONECTES LIMANDA.

The colour-patterns of this species have already been described fully (5), but a brief recapitulation is necessary for purposes of comparison with the other species.

The distribution of the orange and black spots, white spots, and dark patches differs little from that of the generalised scheme (text-fig. 2).

The orange and black spots may occur elsewhere, and usually do so fairly generously. They are small in size, and consist of an orange patch and a semi-lunar strip of black in most instances, although those on the lateral line tend to have the orange surrounding the black. The melanophores on the black area are very large in size (Pl. 33. fig. 3). In the young dab the melanophores on these spots are more numerous, but not of larger size. Epidermal melanophores are present.

The white spots conform to the type fairly closely, but there are usually a few erythrophores present. I have not taken any dabs which had a large number of these spots scattered over the surface in natural conditions. Keeping them on a white background, however, increases the number and size of the spots and also the number of iridophores on them (5, p. 182).

The pale spots are abundant and generally distributed. Apart from the features attributed to this type of pattern, these also show a differential expansion of the melanophores (5, p. 185).

The normal area is divided into a continuous red phase and a discontinuous yellow phase. Neither have epidermal melanophores.

The dark patches are distributed as shown in text-fig. 2, but otherwise are typical.

The dab appears to be found principally on sandy bottoms (2, 3, and 4), and I have never met with any extreme variations in the patterns except those produced in the laboratory. The small size of the spots constituting the patterns, together with their wide distribution and range of tones from black to grey and orange to pale brown, make this fish very suitable for sandy backgrounds. It is evident, however, that it possesses a power of variation which would adapt it to a much wider range of environments than those in which it is most frequently found.

PLEURONECTES PLATESSA.

The plaice is for the most part evenly coloured greyish brown, only three patterns occurring. The orange and black spots are very large and predominantly orange in the adult. The black area is confined to isolated patches, usually in a line running across the orange (Pl. 33. fig. 5). Both areas conform fairly closely to type. The orange area has, however, a large number of iridophores, which probably increase the orange colour by reflecting light through the erythrophores. Epidermal melanophores may be present here in the adult, but not in the young. The black area has very few erythrophores, but the number of the melanophores is slightly higher here than elsewhere, and there are many epidermal melanophores. Only a few iridophores are present.

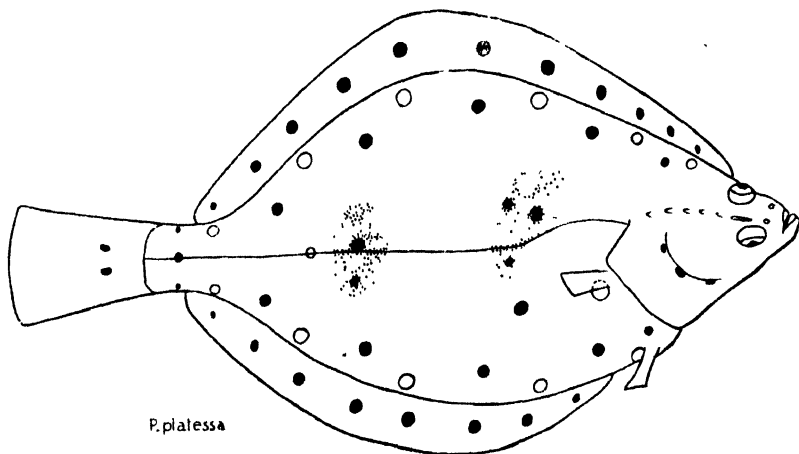
In the young plaice these spots are smaller in proportion to the size of the body, and their form is very like that of these spots in the dab (*cf.* Pl. 33. figs. 3 & 4). Probably the orange area increases in size and surrounds the black area. Intermediate cases indicating this have been seen. These spots occur in the usual positions (*cf.* text-figs. 1 & 3) and also to a certain extent elsewhere.

The white spots when present alternate with the marginal orange and black spots. They have, in the adult, erythrophores besides the usual characters of this pattern. In the young forms, taken on coarse whitish-grey sand, erythrophores were absent from the centres of the spots. In such instances these spots are very numerous, and are scattered all over the surface of the body.

Frequently in the adult and in the young the white spots are almost or totally absent. These specimens were taken from a muddy bottom in estuarine waters. Those kept on a pebbly bottom in the laboratory show these spots developed to a high degree, but I have not seen any like this from natural surroundings.

The dark patches are limited to two on and around the lateral line (text-fig. 3). I have found them much more visible in some specimens than in others under the same conditions.

TEXT-FIG. 3.



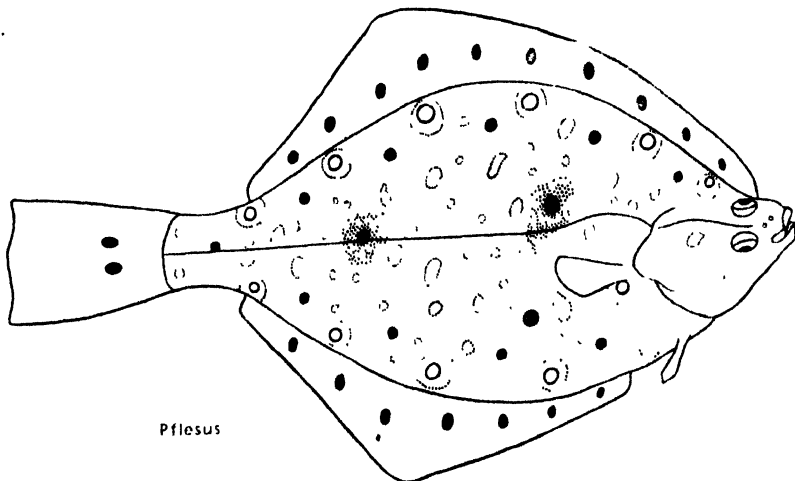
Scheme of constant spots in *Pleuronectes platessa*. Orange and black spots, black; white spots, rings; dark patches, dotted.

The normal area completes the list of patterns, no pale spots or other types being found. It is divided into a red phase and a yellow phase. The former is quite typical, but the latter has many epidermal melanophores, and the dermal melanophores appear to be more expanded than elsewhere. Despite this increase over the usual differences, I could not observe any macroscopic differentiation between red and yellow phases.

It will be seen from the foregoing that in nature, despite fundamental similarities between different forms of this species and the generalised form, there is a very wide range of variation found during the life-history, and, further, that although certain patterns can be developed artificially they may not be normally present. The adult type appears to be uniformly coloured with orange spots and occasional dark patches. The young are, however, very highly marked

with smaller spots closely placed together, and in general resemble the dab. This latter form certainly agrees well with the sandy inshore bottoms on which they are taken. As regards the adult, their principal foods are *Donax* and *Tellina*, and it is possible that the broken and discarded shells on the bottom appear similar to the orange spots on the fish. I have already pointed out the difficulties of determining the habitat, and I think that the occurrence of the food is probably a fairly sure guide. Figure E 1 in Borley's paper (1) is very suggestive (see also his description of Dogger Bank Ground : 2, p. 44). Otherwise the sandy and muddy banks (Day and Couch) fit in well with their uniform tint and absence of pale spots.

TEXT-FIG. 4.



Scheme of spots in *Pleuronectes flesus*. Orange and black spots, black ; white spots, closed rings ; dark patches, dotted ; pale patches, dotted rings.

PLEURONECTES FLEUS.

At first sight flounders appear to be perfectly evenly and darkly coloured with only occasional dark patches. Several patterns exist, however, but they are almost obliterated and are difficult to make out. Yellow takes the place of red in the chromatophores, while the black pigmentation is very dense. Really young forms have not come to hand.

The orange and black spots occupy most of the usual positions, but are sparsely represented elsewhere (text-fig. 4). They are not divided into orange and black parts. The increase in intensity of colour in these spots is due almost entirely to an increase in numbers of xanthophores. Only a few extra melanophores are observed here. Epidermal melanophores are present.

White spots occurring in the usual positions (text-fig. 4) have been found only in forms taken from gravel or sandy bottoms in the laboratory. All other specimens were found on muddy estuarine bottoms, and did not show

any trace of these spots. Where present, however, they are exactly like those of *P. platessa* in minute detail.

There are only two dark patches, both associated with the lateral line (text-fig. 4). These are fairly frequently displayed on a muddy ground.

Certain small pale patches may be observed, firstly, around the white spots (when present) or occupying their marginal positions when they are absent, secondly, scattered all over the body. These are due to an absence of epidermal melanophores, which are otherwise present everywhere else. The general occurrence of these melanophores is very typical of the species. A similar general distribution of the epidermal melanophores was obtained in the dab (5, p. 180) when kept on a black background.

The normal area is similar to type, but the melanic pigmentation is darker than in any other species examined. There are two phases, a yellow with pale xanthophores and with epidermal and dermal melanophores expanded, and a red phase with orange erythrophores and an occasional absence of epidermal melanophores, giving the pale patches mentioned above. These pale patches are much larger in proportion to the size of the fish than are the pale spots of the dab.

On the whole, the tendency in the flounder is towards an even tone with lighter (pale patches) and darker (dark patches) blotches of uneven shape, together with a very decided darkening of tone. This is probably quite a good resemblance to the muddy bottoms found in the usual estuarine habitat of this species (Day and Couch). It has, however, a margin of variation, as shown by the laboratory experiments.

MICROSTOMUS MICROCEPHALUS.

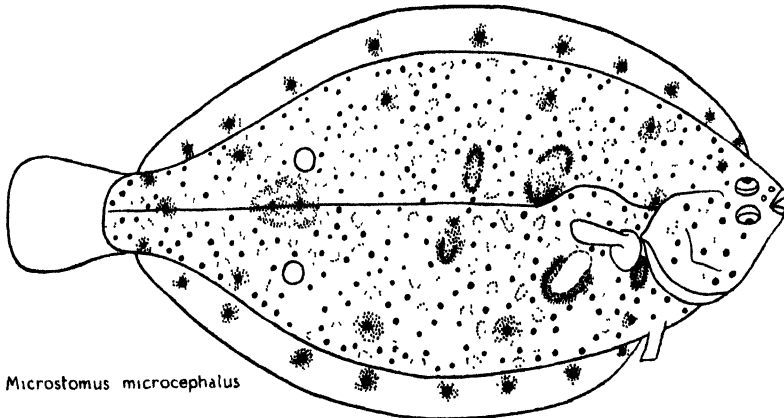
The spots in this species are usually very prominent and generously distributed over the surface. On the whole, they fall in with the generalised scheme, but they are distinctly difficult to homologise. The average colour is yellowish brown, the yellow being more marked in this species than in most others (*cf.* common names—lemon sole, lemon dab).

The orange and black spots are the most prominent, and besides occurring in the usual places, they are scattered profusely over the whole side of the body. These supplementary ones are smaller in size (text-fig. 5). All these spots are divided into orange and black portions. To the naked eye the orange part is dark brown, owing to an increase in the number of dermal melanophores and erythrophores. The black portion lying in the centre and often broken into several pieces (Pl. 33. figs. 6 *a* & *b*) has fewer erythrophores and very many melanophores both dermal and epidermal. The latter appear to be singularly effective in producing a black colour (*cf.* *Pleuronectes flesus*) by reflected light. This is probably due to the fact that they act in two ways: firstly, in absorbing direct light, and, secondly, in absorbing light reflected from the lower tissues. Epidermal erythrophores are also present over the whole spot. From the

diagram it will be seen that only certain of these spots are really complicated in their structure, but these are comparable to the condition in *Pleuronectes platessa* (cf. Pl. 33. figs. 5 & 6 b).

The marginal positions usually occupied by the white spots do not show the characteristic appearance of these spots. These areas are, however, completely free from all other patterns, so that the normal area there present forms a pattern on its own account. Two real white spots are found in a posterior position placed symmetrically with regard to the lateral line. These conform to type, but there are only a few small erythrophores. The large white spot within the curve of the orange and black spot posterior to the pectoral fin differs from the others in having erythrophores in considerable numbers (dotted outline—text-fig. 5).

TEXT-FIG. 5.



Microstomus microcephalus

Scheme of spots in *Microstomus microcephalus*. Orange and black spots (black area), black ; orange and black spots (orange area), dotted ; white spots, closed rings ; peculiar white spot at the base of the pectoral fin, ring with broken line ; pale spots, dotted rings.

The rest of the body is marked with pale spots, which have no erythrophores but show a slight tendency to group the iridophores round the melanophores. This peculiar tendency is also noticed on the normal area, so that it must be regarded as general in the species.

The normal area, which is present in any quantity only in those areas usually occupied by the white spots, is not divided into red and yellow phases. All the erythrophores in this species are orange in colour. Owing to the immense number of spots of the other patterns, the limiting of the normal area almost makes it into another distinct pattern.

This species is said to frequent stones and gravel (Day and Couch), but no detailed information is at hand. Its general appearance would, however, fit in fairly well with this type of habitat.

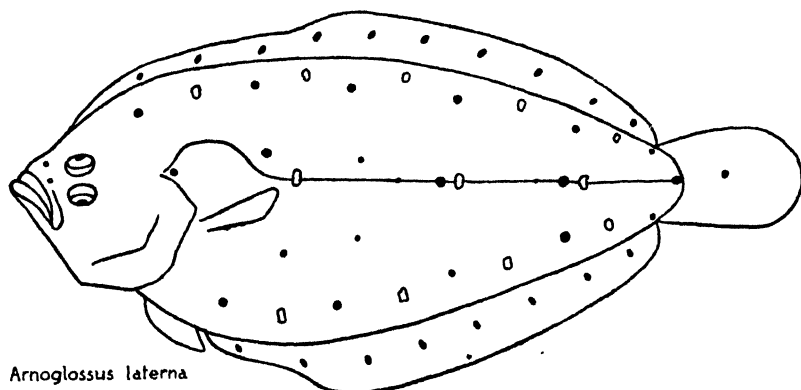
Turning to the Bothidæ, several species have been examined :—

ARNOGLOSSUS LATERNA.

Difficulty was experienced in getting a complete idea of the patterns of this species, owing to the ease with which the scales are removed. A sufficient number of specimens were obtained, however, and a fairly accurate description could be made out. On the whole, the pigmentation is very light indeed, the animal appearing almost transparent in parts.

The orange and black spots occur fairly regularly (text-fig. 6), but they are very small in size. There is no division into black and red parts, melanophores, erythrophores, and xanthophores being present together. The xanthophores are generally towards the centre of the spot. They are all present in largely increased numbers.

TEXT-FIG. 6.



Scheme of constant spots in *Arnoglossus laterna*. Orange and black spots, black ; white spots, rings.

The white spots (text-fig. 6) were found in only two or three specimens. They conform to type, no erythrophores being found on them. No difference in environment could be assumed for their occasional appearance, as all the two dozen specimens were taken in two consecutive hauls over closely adjacent grounds.

Pale spots are present, scattered all over the surface of the body. They are greyish in colour, due to the absence of erythrophores and all but the palest of xanthophores. There is no grouping of the iridophores.

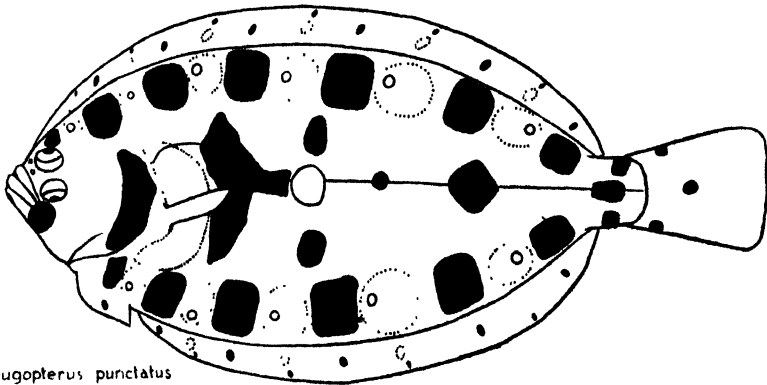
The normal area, which is large in extent compared to the number of spots, is not strictly divided into red and yellow phases. Erythrophores and xanthophores are both present and occur very spasmodically, so that no distinct line exists between a red and yellow phase. The red and yellow pigment is very brilliant, but all pigment-cells are sparsely distributed and no epidermal pigmentation has been observed. This accounts for the pale tone of the

coloration as a whole. The definite habitat of the species is said by Day and Couch to be deep-water sandy bottoms. This accords well with the small size of the spots and the general evenness of the tone with slight variations to grey (pale spots) or brown (normal area). I have found no dark patches, and, apart from the occasional white spots, there are no "facultative" spots. There does not appear to be any great degree of variation, which agrees with the very localised distribution of this species.

ZEUGOPTERUS PUNCTATUS.

In this species the main patterns appear very large and bold with irregular outlines, and are so arranged dorso-ventrally that a banded appearance is noticeable, the lateral line spots lying more or less directly between the marginal spots. A greenish-brown tinge is found occasionally, while in other areas a reddish shade occurs.

TEXT-FIG. 7.



Zeugopterus punctatus

Scheme of constant spots in *Zeugopterus punctatus*. Orange and black spots, black; white spots, closed rings; pale spots, dotted rings.

The orange and black spots are very large dark areas centred in the usual positions (text-fig. 7). Within them can be found other patterns such as the pale spots, which probably indicates that they have spread out from a central point and enclosed other preformed spots. Dermal melanophores, erythrophores, and xanthophores are in great numbers, the former being rather larger than usual. Epidermal melanophores and erythrophores are also found occasionally. There is no division into red and black areas. These spots are sharply marked off from the neighbouring patterns (Pl. 33. fig. 2).

Small white spots are arranged marginally, and one large one on the lateral line lies between the orange and black spots. These white spots have no erythrophores or xanthophores, but there are very many iridophores with the usual grouping. Around each of these spots is a pale patch which, while showing a slight grouping of the iridophores, is not extreme in this respect,

and erythrophores may be present, giving the spots a yellowish tint. These patches are large and intensify the barring effect produced by the orange and black spots. There is one pale patch at the base of the pectoral fin without the usual white spot in the centre. This has more grouping but few erythrophores, although xanthophores are present in considerable numbers.

Small pale spots are present all over the surface, even within the orange and black spots. They have no erythrophores or xanthophores and conform to type.

The rest of the surface, which is restricted, consists of normal area, which is not divided into red and yellow phases. The two types of cell grade into one another, the erythrophores being at the edge of the scales.

Day and Couch both speak of the habitat of this species as being on low shelving rocks near sandy bays, covered in seaweed. Day says that they are difficult to find in aquaria. This may well be true in nature as well, since their irregular banded appearance with a greenish-brown tinge render them invisible among seaweed on such a substratum.

RHOMBUS MAXIMUS and R. LÆVIS.

I have not been able to obtain sufficient material of these species to give a complete account of the colour-patterns, but certain interesting points stand out.

Both are very similar in their colour-patterns. Over the whole surface of the body these patterns are scattered in great abundance, and, although in young turbot (6-7 cms.) white spots of considerable size occupy the usual positions and orange and black spots lie in between them, in the adult there are so many others all around them that it is impossible to discriminate between "primary" and "secondary" spots. The orange and black spots are interesting in their minute structure. There is a general increase in numbers of melanophores and, in the centre of the spot, of erythrophores, but the edge is darkened by the absence of these last and by the presence of epidermal melanophores. This outer ring or black area is usually broken up into small pieces rather like those in *Microstomus microcephalus*. If the ground-colour is pale then the whole spot is dark and relatively large, but if the ground-colour is dark only these small black areas are noticeable.

A similar arrangement is found in the white spots whereby one pattern may produce both large and small spots. The centre of the white spots is of the typical form, no erythrophores being present, but around the margin of the spot the iridophores are very numerous and have spread on top of the melanophores, so that an expansion of the melanophores does not screen the iridophores as usual. Thus these small marginal areas of the white spots are rendered non-facultative and always appear white.

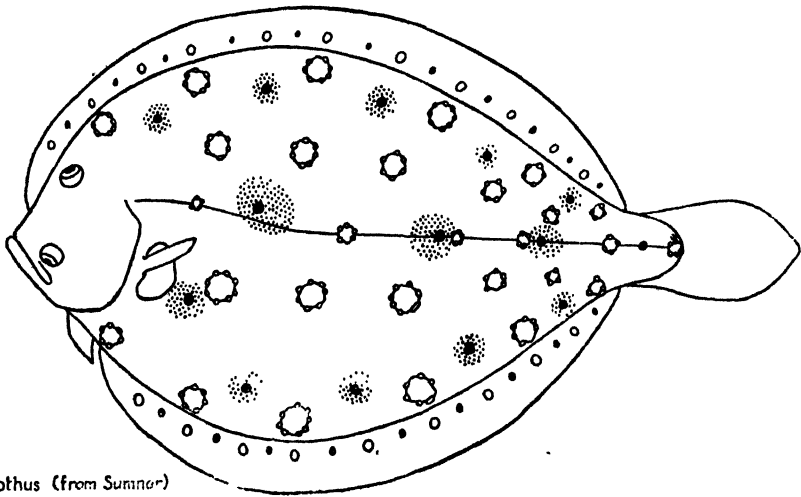
The general surface of *R. lævis* is very complicated, and there appear to be pale spots without erythrophores and red and yellow phases in the normal

area. The orange and black spots and white spots are the most prominent, and it is suggestive that two species of fish, both much addicted to wandering (Day), should have developed patterns which can be used either for a coarsely or for a finely divided bottom.

BOTHUS PODAS*.

Sumner's description of the patterns of this fish (9, pp. 414-416) fits in extraordinarily with the general scheme. In text-fig. 8 I have diagrammatised the colour-pattern from his photographs and from his description.

TEXT-FIG. 8.



Bothus (from Sumner)

Scheme of constant spots in *Bothus podas*. (From Sumner.) Orange and black spots, black; white spots (annuli), small rings; white spots (intra-annular areas), large rings; dark patches, dotted.

His "pale spots" correspond to the white spots, and if they are at all comparable with those of *Rhombus laevis* a ready explanation is given for his "anuli," which never wholly disappear.

The orange and black spots are directly comparable with those of *R. laevis*—"a dark ring with a paler centre," but all darker than the ground-colour.

The "dark blotches" occupy the positions of the dark patches and behave in exactly the same way. The other "vague and impermanent arrangements" probably refer to the generally distributed pale spots.

The specimens of this species obtained by Sumner came, he believed, "from dark mixed sand of lava and tufa" and from bottoms "diversified by white shell fragments"—a fairly wide range.

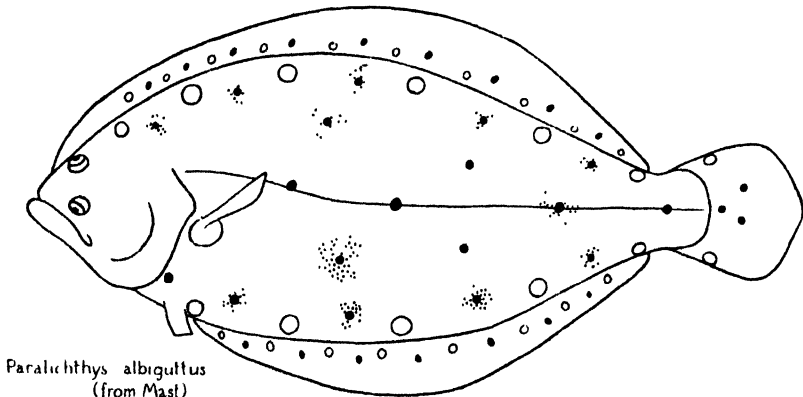
* Sumner refers to this fish as *Rhomboidichthys podas*, and includes in it those described by Canestrini and others as *Rhombus podas* and *Rhombus rhomboides*.

PARALICHTHYS ALBIGUTTUS.

It is obvious from the diagrammatised drawing (text-fig. 9), composed from the photographs in Mast's paper (6), that this species also conforms in distribution to the generalised scheme. It is in appearance remarkably like the dab (*Pleuronectes limanda*), the spots being of similar size and distribution. It appears to be a good case of convergence, possibly owing to a similarity of environment, as Mast states that his specimens were taken on sand.

So far it has been possible to refer to the generalised scheme, but in *Solea vulgaris* and apparently in the Soleiformes generally (from fairly careful illustrations—not photographs) there is not the same strict adherence to it.

TEXT-FIG. 9.



Paralichthys albiguttus
(from Mast)

Scheme of constant spots in *Paralichthys albiguttus*. (From Mast.) Orange and black spots, black; white spots, rings; dark patches, dotted.

SOLEA VULGARIS.

The general pigmentation is very dark, and under a number of diverse temporary conditions only a few patterns have been seen. Nothing approaching the appearance or constitution of the orange and black spots was found. The most prominent markings are the dark patches, which are very numerous and lie in five rows (text-fig. 10). They are rectangular in shape but irregular in outline, and behave exactly like the dark patches in the other species examined. Their appearance is due solely to a differential expansion of the chromatophores.

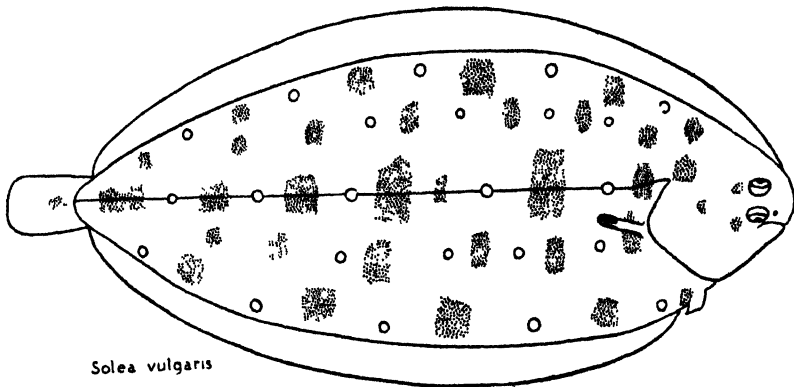
The only other pattern found consisted of white spots lying in between most of the dark patches. These were present only in some specimens, and I have never found them made use of, the melanophores being expanded and covering the iridophores. The latter cells are in considerable numbers, but are not grouped. Orange erythrophores are also present.

The rest of the surface is normal area of a dark brown hue. No xanthophores were found, the erythrophores being orange.

On the whole, I do not think that the patterns ever conformed to the generalised scheme I have put forward for the others. This opinion is strengthened when some of the Indo-Pacific forms described by Norman (7), with many transverse bars across the body, are taken into account.

In the general body-colour and in the absence of the smaller definite patterns this fish resembles *Pleuronectes flesus*. Its habitat is also somewhat similar. Day gives sandy and gravelly (possibly accounting for the retention of the white spots) bottoms with occasional excursions up estuaries, presumably into muddy surroundings. When trawled they usually have sand and mud adhering to them on their upper surface.

TEXT-FIG. 10.



Scheme of constant spots in *Solea vulgaris*. White spots, rings; dark patches, dotted.

PSETTODES ERUMEI and *P. BELCHERI*.

Although I have not been able to examine these species microscopically, the distribution of their patterns is sufficiently interesting to warrant description.

In the young forms (10–11 cms.) only transverse bars can be seen (Pl. 34. fig. 2). These appear to partake of the nature of dark patches, and remind one strongly of the bars in the perches, which, like the dark patches, are facultative and completely disappear under certain conditions*.

In the adult (20–30 cms.) these bars persist, but in addition spots having the characters and distribution of the orange and black spots and white spots are seen (text-fig. 11). Their distribution is irregular and the figure is somewhat too schematic. This may be due, of course, to the insufficiency of material and lack of the proper fixation and technique to obtain the best results. On the other hand, it may indicate that the regular distribution of these patterns, so characteristic in the other flat-fish, has not yet been stabilised in these

* *Perca fluviatilis* kept on a pure white background becomes intensely pale, the bars being invisible. When the fish is excited by attempted capture, however, the bars immediately reappear.

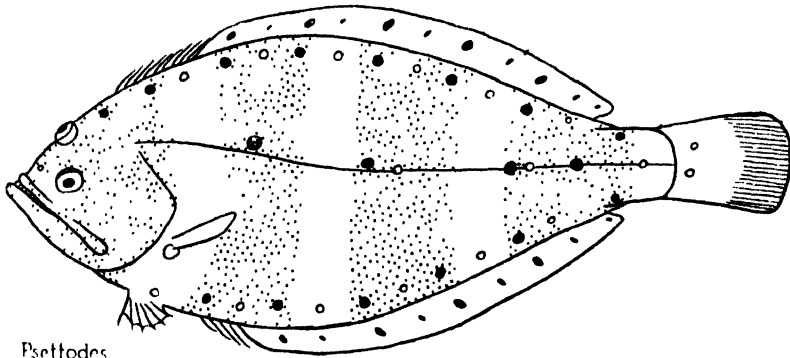
more primitive forms. The white spot at the base of the pectoral fin should be noticed particularly, as it is present in all other species I have examined except *Solea vulgaris*.

The exact habitat is not known, but they are confined to the Indian Ocean and Persian Gulf.

DISCUSSION.

From the foregoing descriptions there can be little doubt as to the ancient nature of the distribution of the specialised spots, such as the dark patches, orange and black, and white spots. This special arrangement is present in

TEXT-FIG. 11.



Psettodes

Scheme of constant spots in *Psettodes crumci* and *P. bulcheri*. Orange and black spots, black; white spots, rings; dark bars, dotted.

all Pleuronectiformes, fairly constant in *Psettodes*, and possibly rudimentary in Soleiformes. Of the latter I am not at all certain, particularly as the Soleiformes may not be related directly to the Psettodoidea.

It may be argued that since these spots also occur generally this is the primitive condition and the specialised secondary. In development, however, the reverse is the case, the general spots being secondary. This specialised distribution is probably due to some deep-rooted cause akin to symmetry.

The other patterns variously designated as pale spots, pale patches, and red and yellow phases of the normal area are by no means so frequently present, and are probably recent or specific additions to the fish's range of markings.

Starting with the young *Psettodes*, we find a vertical barring effect similar to the perches. This is followed by a tendency to break up the bars by means of the orange and black spots and the white spots in the adult. The vertical bars are not harmful (and may be protective) in a vertically swimming fish with only the vertical shadows to hide in, but this break-up of the surface is essential, except in very special circumstances, to a fish lying closely on the bottom. That a barred effect can still be maintained under certain conditions

is shown conclusively by *Zeugopterus punctatus*, which has reproduced the barring in a specialised environment. It should be noticed that the dark bars here consist of enlarged orange and black spots, and not of dark patches.

The facultative bars in the Psettodoidea are broken up into the dark patches in the higher forms. Thus by the modification of the existing bars and by the production of two new patterns arranged in dorso-ventral symmetry (which is not so regular or exact as lateral symmetry) the Pleuronectidæ present a spotted and blotched appearance instead of a barred one. It should be noticed that the orange and black spots are always "inside" the white marginal spots, so that few definite lines are formed.

Having seen, then, the extent to which the species of Pleuronectiformes are committed by reason of their phylogenetic relations (namely, a pattern of dark spots—orange and black—along the margin and lateral line, a pattern of white spots in similar positions, and a series of dark patches associated with the dark spots), we can proceed to a consideration of the agreement between the general effect of patterns in particular species and their normal environment.

Enough has been said to show that the agreement is considerable and is attained in more ways than one.

First, by means of specialised patterns of appropriately sized and coloured spots a close approximation to a limited type of background has been attained. *Arnoglossus laterna* and *Zeugopterus punctatus* are examples of this. Several of the fixed or non-facultative patterns in other species such as *Pleuronectes limanda* and *P. flesus* also come into this category, although all the patterns of these species do not.

Secondly, the faculty for wide variation in the development of patterns is shown to be possessed by many forms. For example, the white spots in the adult *Pleuronectes platessa* are usually absent, although numerous in specimens kept on whitish pebbly bottoms and in the young forms which normally inhabit inshore sandy grounds. It should be noted that this variation is not due to expansion and contraction of the chromatophores, but to an increase or decrease in the numbers of chromatophores in the patterns concerned. It is therefore semi-permanent, the fish being able to reverse or further alter its battery of patterns later on upon being placed upon or moving to another background. This type of variation takes time to mature, and appears most frequently in species having different habitats at different periods of the life-history, so that a considerable time is available for the appearance of the modified patterns.

Thirdly, we find that there are patterns of the facultative type developed which can be used at the will (apparently) of the fish and which appear visible only under certain conditions. The white spots of *Pleuronectes limanda* (and others) are thus displayed when the fish is placed on a pebbly bottom with shell fragments. This adjustment only takes a few seconds in many cases, and is due to the expansion and contraction of the chromatophores.

As an elaboration of this type of variation the white spots in *Rhombus lævis* may be taken. This species, by a subdivision of the facultative spot, has

produced a mechanism which can be used on two widely differing bottoms. I have pointed out that *R. laevis* is a highly vagrant species, and it appears probable that these facultative arrangements are definitely advantageous to fish accustomed to roam over a variety of grounds.

It is clear that, since the semi-permanent production of spots and the facultative appearance of patterns are convenient to the habits of the species, they must be regarded as adaptations quite as much as specialised patterns which agree with the appearance of the localised habitat.

Here, then, is the answer to the first problem so far as it concerns the species studied in detail: that the species endowed with ancestral patterns, consisting of dark patches, dark (orange and black) spots and white spots distributed in a particular way, but with a wide range of minute structure possible, are in most cases closely adapted to their environment.

Turning now to the details of the patterns by which these adaptations have been carried out, we find several well-defined lines of development.

On the dark side we find the fairly small orange and black spots evolving, firstly, by an increase in the pigmentation generally (e. g., *Pleuronectes flesus*, *Arnoglossus laterna*, and *Zeugopterus punctatus*; Pl. 33. figs. 1 & 2), and then by a division of the spot into red and black areas (e. g., *Pleuronectes limanda* and *P. platessa*; Pl. 33. figs. 3, 4, & 5), opening up possibilities of elaboration and subdivision such as are found in *Microstomus microcephalus* and *Rhombus laevis* etc. (Pl. 33. fig. 6).

The dark patches which are facultative are apparently derived from the dark bars of the Psettodoidea. In many Pleuronectoidea they are lost or at any rate very limited in their distribution.

The evolution of the white spots is very similar to that of the orange and black ones. The first point is an increase in the number of iridophores, and although I have found no example in which this is separated from a grouping of the iridophores round melanophores and a differential expansion of the latter, I am inclined to separate the non-facultative white spot with many iridophores from that which can appear and disappear by reason of the melanophore control. The usual condition would therefore represent two stages in the evolution of these spots (Pl. 34. fig. 1 c). Subsequently the erythrophores become scarcer (*Pleuronectes limanda*), and finally absent (*Arnoglossus laterna* and *Zeugopterus punctatus*; Pl. 34. fig. 1 d).

Again, we find the phenomenon of subdivision of a spot. In *Rhombus laevis* the annuli have so many iridophores that they are now non-facultative, at the same time making the spot useful on two backgrounds.

Lastly, we have the generally distributed pale spots and patches. These are grouped together because they are of similar function, having a small size and a general distribution. On the other hand, they are produced in different ways. The pale spots primarily have no erythrophores (*Pleuronectes limanda*, *Arnoglossus laterna*; Pl. 34. fig. 1 a), and a slight tendency to grouping is seen in *Microstomus microcephalus* and *Zeugopterus punctatus* (Pl. 34. fig. 1 b). This may mean a different origin and have no evolutionary significance. The

pale patches of *Pleuronectes flesus* are due to a lack of epidermal melanophores, while those of *Zeugopterus punctatus* occupy a position halfway between the white and pale spots in that species, with a definite increase in the number of iridophores.

Thus it will be seen that the pale spots and patches are probably of recent evolution, and do not show that close series of forms found in the case of the other patterns. They probably represent recent reactions of the species to their particular environments.

It has already been shown that uniform backgrounds produce a uniform adaptation immediately by the expansion or contraction of the chromatophores. This is subsequently consolidated and improved upon in the course of a few weeks by an increase or decrease in the number of chromatophores (5, pp. 180-183) *. These latter processes are exactly those producing the patterns in the semi-permanent adaptations, according to the evolutionary trend outlined above. Thus it would appear that factors in the environment producing temporary adjustments also produce more permanent effects of a strictly structural character. It is not too much to suppose that the continuance of a constant environment (or background) over very considerable periods would render those patterns more fixed. There is always retained the ability to alter the general shades and tones by the expansion or contraction of the chromatophores.

This accounts, then, for all the adaptations mentioned above except those of a facultative nature. These appear to be of a purely physiological character, and a full understanding of their evolution and development will not be possible until more detailed knowledge of the mechanism of control is obtained.

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* I would quote also the work of Sumner and Mast; but Sumner does not appear to have kept his fish for long on any particular background, and Mast has not given microscopical details, so that it is not possible to be sure what his altered patterns represent. Cunningham and McMunn's paper helps a little here, although their observations (directed to another purpose) are not quite complete enough (10).

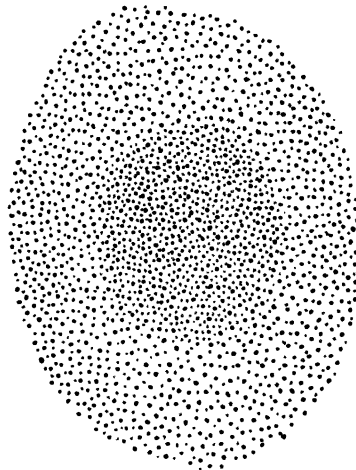


Fig. 1. *P. flesus* (adult)

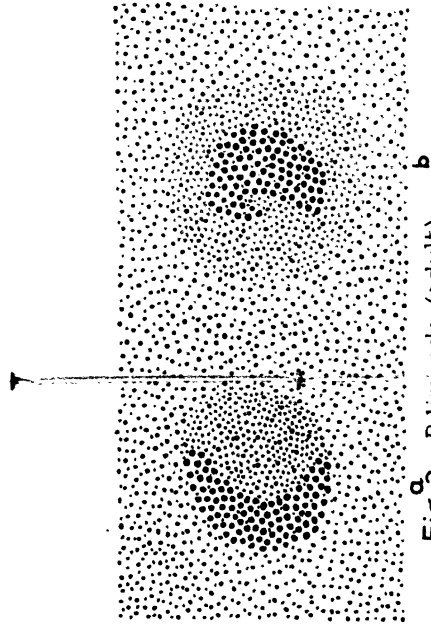


Fig. 3. *P. limanda* (adult)

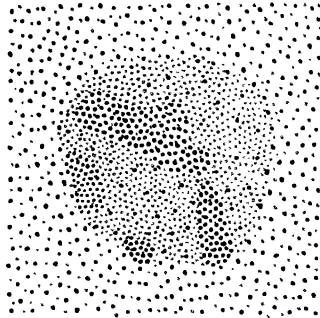


Fig. 5. *P. platessa* (adult)

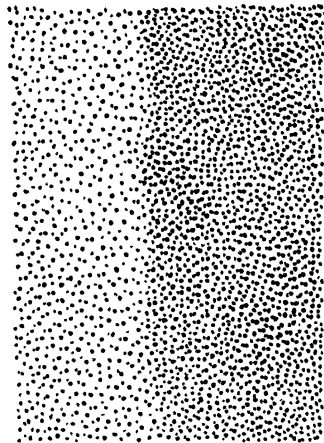


Fig. 2. *Z. punctatus* (adult)

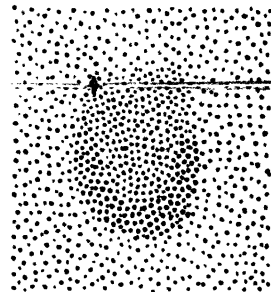


Fig. 4. *P. platessa* (young)

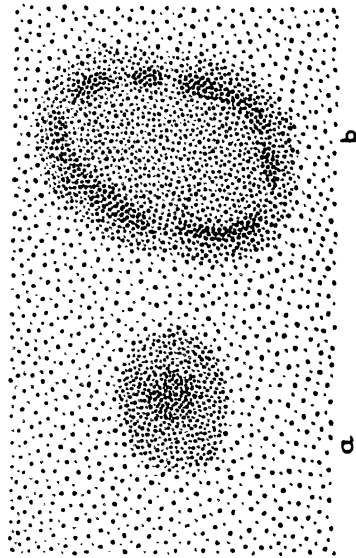


Fig. 6. *Microstomus. microcephalus* (adult)

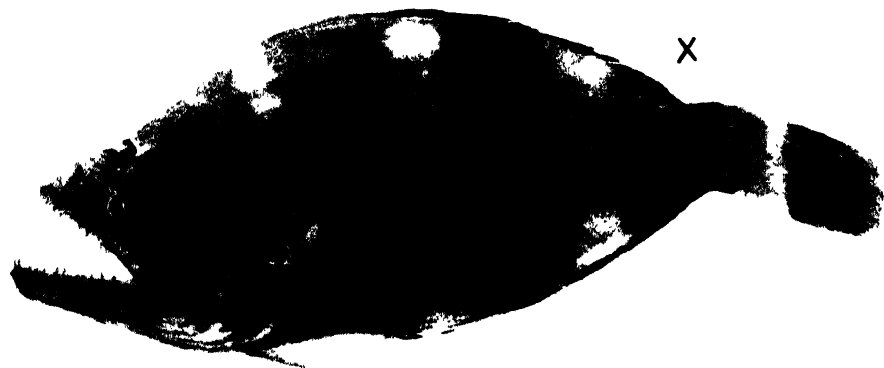
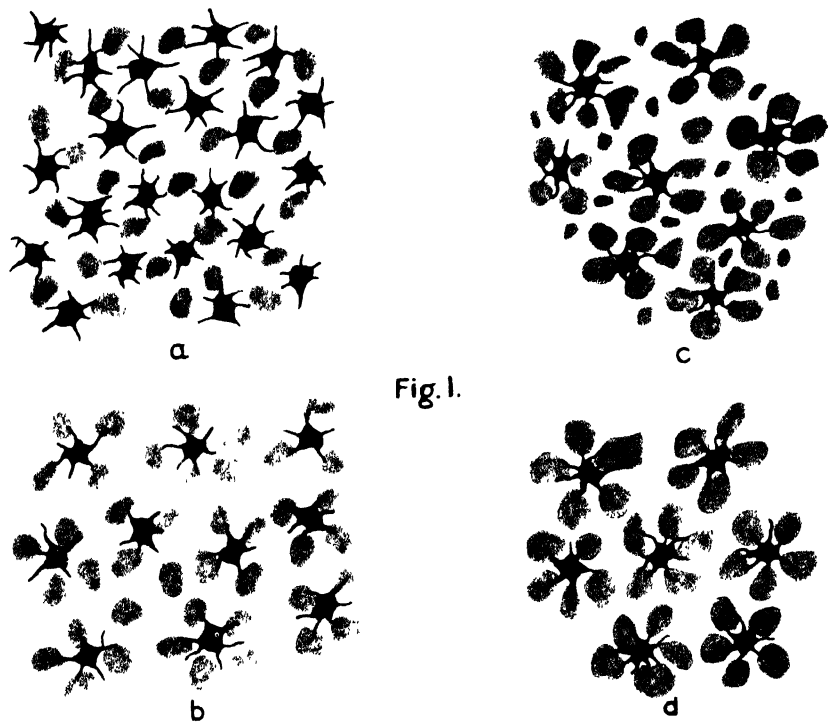


Fig.2.

EXPLANATION OF THE PLATES.

PLATE 33.

Figs. 1-6 are schematic representations of the orange and black spots in several species of flat-fish. Black dots represent melanophores, orange dots erythrophores and xanthophores. Each orange and black spot is accompanied by a patch of normal area for comparison. No attempt has been made to give actual numbers of chromatophores, but the proportions are indicated fairly accurately.

- Fig. 1. Orange and black spot of *Pleuronectes flesus*, showing an increase in the number of erythrophores.
- Fig. 2. Orange and black spot of *Zeugopterus punctatus*, showing an increase in the numbers of melanophores and erythrophores.
- Fig. 3. Orange and black spots of *Pleuronectes limanda* (adult), showing division into red and black areas with many erythrophores on the former and large melanophores on the latter.
- a. Spot in which the red area extends only on one side of the black.
 - b. Spot in which the red area surrounds the black.
- Fig. 4. Orange and black spot of *Pleuronectes platessa* (young), showing division into red and black areas and an increase in the numbers of erythrophores and melanophores respectively (cf. fig. 3 a).
- Fig. 5. Orange and black spot of *Pleuronectes platessa* (adult), showing the growth of the red area around the black, characteristic of this species (cf. fig. 3 b).
- Fig. 6. Orange and black spots of *Microstomus microcephalus*, showing the red area with an increase in the numbers of melanophores and a great increase in the numbers of erythrophores, and the black area with a greater increase in the numbers of melanophores.
- a. The simple type of spot.
 - b. The complex type with broken black area.

PLATE 34.

- Fig. 1. To illustrate the constitution of the pale spots and the white spots. Iridophores are indicated in grey, as they appear in transmitted light.
- a. The condition in the pale spots of *Pleuronectes limanda* and *Arnoglossus laterna*. No erythrophores.
 - b. The condition in the pale spots of *Microstomus microcephalus* and *Zeugopterus punctatus*. No erythrophores and a slight tendency to grouping.
 - c. The condition in the white spots of *Pleuronectes platessa*. Definite grouping.
 - d. The condition in the white spots of *Arnoglossus laterna*. Definite grouping and no erythrophores.
- Fig. 2. Photograph of a young specimen of *Psettodes erumei* (10 cms.). Note the presence of very definite barring and the absence of other spots. This barring is very similar to that in the perches. At the point indicated by a × can be seen the characteristic Y-shape of a bar present in most of the perches.

The Development of the External Features of *Xenopus laevis*, based on Material collected by the late E. J. Bles. By Prof. KARL PETER, University of Greifswald, Germany. (Communicated by G. R. DE BEER, M.A., B.Sc.)

(PLATES 35-39 *.)

[Read 23rd October, 1930.]

IN his excellent paper, "The Life-History of *Xenopus laevis*," the late Edward J. Bles described the development of this remarkable Aglossan. He treated *in extenso* of the earliest stages—fertilization, segmentation, gastrulation—and more briefly of the development, after hatching, of the mature larva and of the metamorphosis. The communication was "intended to be the first of a series dealing with observations on the life-history of the Anura Aglossa and their anatomy at different stages of development." Bles obtained by breeding in captivity a large collection of the eggs and larvæ of each stage, which is now preserved in the Embryological collection of the Department of Anatomy in Cambridge. There are also some fine pictures, of which a number are unfinished, of larvæ of *Xenopus* from the master-hand of Mr. Maxwell.

Impaired health, unfortunately, prevented Dr. Bles from completing his scheme of investigation, and his Trustees have asked me to give a description of Maxwell's drawings—an invitation which I have accepted with great pleasure. But these drawings do not represent the entire development of *Xenopus*: a few only of the larvæ had been depicted in various aspects with great skill and delicacy.

To complete the description of the development of this interesting species, I found it necessary to have the lacking stages drawn after Bles's material. Therefore I add to the drawings of Maxwell a fifth Plate in the manner of a "Normentafel" containing the larvæ from the stage just before hatching up to that of the young frog. The youngest stages are represented in Bles's own paper. Bles's fig. 14 is almost the same stage as our fig. 1, Pl. 39.

The larvæ of Pl. 39 are drawn by Herr Levin under my direction. They are well preserved, except that a few of the older ones are a little shrunken. These deformations are corrected.

The larvæ of Pls. 35-38 are pictured at a higher magnification than those of Pl. 39, and were drawn after the living specimens. They show more details than the preserved tadpoles. As Bles says in his paper, the living larvæ are very transparent; in the head-region almost all of the complicated structure of the vertebrate head can be studied in the living animal.

* Pls. 35-38 drawn under the direction of E. J. Bles.

The larvæ of figs. 1-12, Pl. 39, are seen from the left side, the little frog fig. 13 from the dorsal side. Figs. 1 a-12 a show the anterior end of the larvæ: 1 a-5 a from beneath, ventrally; 6 a-12 a from above, dorsally.

The drawings of Maxwell represent older larvæ and frogs. The tadpole of Pl. 38, fig. 3 and Pl. 35 is a little younger than Pl. 39, fig. 6. It is drawn from the right side, from below, and from above. The figures of Pl. 36 show a larva in the same aspects; it is a little younger than Pl. 39, fig. 7. In Pl. 37 a tadpole between stages 7 and 8 of Pl. 39 is represented. Pl. 38 shows a young frog, older than that of fig. 12, and the anterior end of a full-grown frog.

The description of the Maxwell drawings is interpolated between the corresponding stages of Pl. 39.

Before entering on the description, I have to thank Professor Wilson and Mrs. Bles for the confidence they have shown me by entrusting me with this work and for the munificence which has enabled me to utilize the whole material. I made a preliminary survey of it in the Anatomical Dept. in Cambridge, and am under obligation to Dr. Shearer for kindly assisting me in this labour. At Greifswald I studied the material intensively, chiefly with regard to the development of the external features, and had the figures drawn which form the "Normentafel" in Pl. 39. I hope later to be able to supply further papers illustrating the internal development of *Xenopus*.

Description of the Larvæ.

PLATE 39. FIGS. 1 & 1 a.

The larva has a length of 4.7 mm. It is at the same stage of development as the larvæ represented on fig. 14 of Bles's paper. It is still enclosed within the egg. The tail is short, only one half of the length of the body of the larva; the fin-fold is well developed.

The exterior shows very few differentiated features. The head is separated from the body by a slight constriction (fig. 1 a). The swelling in front of this constriction shows three tubercles, the buds of the external gills. The dorsal protuberance contains the eye.

In the front of the head protrudes the cement-organ (the "Haftnapf"); it consists of a pigmented ovoid area. Dorsally from the cement organ, separated by the slight depression of the stomodæum, lie the frontal glands, the "Stirnstreifen" of German authors, the organs which soften the egg-membrane during hatching. Beneath the lateral side of this dark stripe are the small nasal pits.

In the living specimen the eye and the myotomes of body and tail are better visible than in the preserved one (cf. Bles's fig. 14).

PLATE 39. FIGS. 2 & 2 a.

Fig. 2 represents a larva of 6 mm. length after hatching. The tail has grown longer, up to one-third of the length of the whole larva; its end is not yet

sharp ; the fin-fold is broader. In the body and tail the myotomes are visible, although not very distinctly.

The head is further developed and shows more details. Two stumps of external gills are developed ; the pigmented eye and the nasal groove are visible. The still imperforate stomodæum, which is a deeper depression than at the earlier stage, lies ventrally from the nasal pit. The cement-organ protrudes sharply : its glandular area shows a short bifurcation : it is bilobed, and the surrounding region is pigmented. Bles says that the form of the glandular area is crescentic. The frontal gland is almost invisible, only a delicate pigmentation shows its position.

PLATE 39. FIGS. 3 & 3 a.

The larva of fig. 3 is 7.6 mm. in length, three-fifths of it belonging to the tail. The end of the tail is more acute than in the former stage : the fin-fold is much broadened. The myotomes are distinctly pronounced. From the dorsal side of the head black pigment-cells extend to the tail.

The body of the larva has become thicker, shorter, and better delimited from the tail. The cloaca ending in the anus is visible at the postero-ventral end of the body.

Three gills are developed, short and without bifurcation. Behind them a slight protuberance indicates the position of the pronephros.

The mouth is now perforated. It lies dorsally from the bilobed cement-organ, which is well developed.

PLATE 39. FIGS. 4 & 4 a.

Fig 4 shows a well developed tadpole. The tail has lengthened, both absolutely and relatively. It occupies two-thirds of the whole length, and has reached its definitive size.

The pigmentation spreads out over the body and the entire tail, leaving free the ventral side of head and body.

The gut begins to curl up, the cloaca has become longer. Through the transparent skin the heart is visible in front of the gut.

The external gills are at the height of their development ; three threads, simple, without branches, are to be seen. As the ventral view (fig. 4 a) shows, the operculum begins to grow over the gills.

On the top of the head are to be seen the very prominent cement-organs, the stomodæum and the nasal pits. The pigmented area of the cement-organ has a pronounced crescentic shape. The mouth is perforated and has a curved form. On its edge a little white spot is to be seen, the place from which the tentacles grow out.

PLATE 39. figs. 5 & 5 a.

The stage of fig. 5 is characterized by the reduction of the external gills and the cement-organ. The length of the tadpole is 9.5 mm. ; head and body occupy one-third of it.

The tail with the fin-fold has not altered its relative length and its shape, except that the dorsal fin-fold has no longer the breadth of the ventral one.

In this specimen the pigment-cells are expanded. They spread out over the dorsal side of the body and root of the tail; the rest of the tail is pigmented all over.

The gut is arranged in several coils; its antero-dorsal point is covered by the bud of the pronephros, which is better visible than in the former stage.

The external gills are very much shortened; they are partly covered by the operculum. Only two short stumps appear from under the spiraculum. The heart is situated between the gill-regions.

The anterior end of the head becomes broader. The mouth is also broad, and at its sides there are sharp edges; these little points are the beginnings of the tentacles. The mouth lies on the upper side of the head. The cement-organ is in regression and is only faintly pigmented.

PLATE 35. FIGS. 1 & 2; PLATE 38. FIG. 3.

In Pl. 35 and in Pl. 38 is drawn a larva of the stage between figs. 5 & 6 of Pl. 39.

Pl. 38. fig. 3 shows the fore end of the tadpole from the right side under higher magnification; Pl. 35. figs. 1 & 2 represent the same specimen from the dorsal and the ventral sides. The figures, drawn from a living larva, show very well the external features and the transparency of the body; almost all the organs of head and body are visible through the skin, with vessels, nerves, and muscles.

The head has now the shape of a chisel. It is broad and flat. The lower lip overlaps the upper, the mouth lies on the dorsal face of the snout. At the edges of the mouth protrude short stems, the buds of the tentacles.

The side view shows the ears, the heart, and the spiracle. No external gills are visible; they are completely atrophied. The filters of the gill-chamber shine through the skin. Of the extremities there is no trace. The gut is full of iridescent material; at its dorsal anterior edge lie the curved tubules of the pronephros. The myotomes of the tail are well pronounced.

The distribution of the pigment-cells is similar to that in Pl. 39. figs. 5 & 6. In the skin they are contracted, in the brain-membranes expanded (*cf.* the dorsal aspect, Pl. 39. fig. 1).

This figure shows the breadth of the head and the short rudiments of tentacles widely distant one from another. The lobi olfactorii, with the nervi olfactorii which diverge towards the pigmented nostrils, are distinguishable in the brain, and further back the epiphysis with its pedicle, the mid-brain, and the rhombencephalon. On both sides of the latter are the ear-vesicles, partly covered by pigment-cells.

The tubules of the pronephros are situated laterally from the gut. The vesicle behind them is probably the lymph-heart.

The ventral aspect (Pl. 35. fig. 2) shows the gut, and in front of it the heart. From the bulbus emerge the aortic arches, which spread out laterally. They lie over the gill-chamber, whose filters are faintly visible.

PLATE 39. FIGS. 6 & 6 a.

The larva of fig. 6 shows several differences from fig. 5; the end of the tail sharpens, the gut curls up, the gills disappear, the head flattens dorso-ventrally.

The length of the tadpole is 14 mm. The specimen of fig. 6 is a little shrunken (see the folds of the submental lymph-sac).

The head has the shape of a chisel, flattened dorso-ventrally and broadened transversely, as fig. 6 a shows. In this figure the larva is seen from the dorsal side, the ventral side exhibiting no interesting detail after the disappearance of the cement-organ. The broad mouth is dorsally situated; at its edges are two short threads, the tentacles. The circumference of the nostrils is pigmented, likewise the brain.

The external gills are completely atrophied; no trace of them is visible.

The gut is disposed in several coils. Between the cloaca and the tail a little knob represents the first rudiment of the posterior limb. The bud of the anterior extremity is a rounded thickening at the anterior end of the gut.

The point of the tail is thinned; the dorsal fin-fold is narrow, the ventral one much broader.

PLATE 36. FIGS. 1-3.

This tadpole, a little older than that of Pl. 39. fig. 6, is pictured in three aspects—from the left (fig. 3), from the dorsal (fig. 2) and from the ventral side (fig. 1).

Fig. 3 shows the larva in full length from the left side. The shape of the body has not altered; the ventral fin-fold of the tail is very broad for the greater part of its extent, but becomes rapidly narrower towards the hinder end. The end of the tail is very acute.

The tentacles are but short. The limbs are little protuberances without further differentiation. Ventrally from them are the coils of the gut, in front of them the gill-chamber.

The dorsal aspect shows the same organs in head and body as Pl. 35. fig. 1. Note the little lymph-heart dorso-medially from the pronephros.

Seen from the ventral side (fig. 1) the larva shows the curled-up gut, and in front is the heart with the aortic arches. The filter-processes in the gill-chamber are distinctly visible.

PLATE 39. FIGS. 7 & 7 a.

The larva acquires the outlines characteristic of a *Xenopus* tadpole. It has become a great deal longer—the length is 29 mm.

The pigmentation shows the characteristic distribution found by Bles; it covers the dorsal half of the animal, except for a dorso-lateral stripe on each side of body and tail. But the end of the fin-fold shows fine black pigment-cells.

The skin shows a new feature : the sense-organs are faintly visible in the skin covering the gut and in the fin-fold between the gut and cloaca.

The head is broad and dorso-ventrally flattened. The mouth is a little widened. The tentacles have been growing out of its edges ; they are longer than in fig. 6 and bifurcate at their ends.

The dorsal side (fig. 7 *a*) shows the broad expanse of the snout and the brain shining through the skin. From the anterior end of the brain emerge the olfactory nerves to the nasal pits. A white spot indicates the position of the epiphysis.

In the lateral aspect note the open spiracle.

The buds of the extremities are more conspicuous. The anterior one appears as a short stem under the skin, the posterior one is well developed ; neither is yet differentiated into leg and foot.

PLATE 37. FIGS. 1 & 2.

This tadpole drawn by Maxwell and represented in Pl. 37 from the left and from the dorsal sides is to be placed between fig. 7 and fig. 8 of Pl. 39.

The head is very broad and flat, like a chisel. The mouth-region between the tentacles shows a straight contour (fig. 1). The body is broad and flat too ; in the region of the extremities it suddenly becomes narrower. The tail is very flat from side to side and sharpens at the end.

The tentacles are long ; the left one is apparently broken off ; the right one bears a short branch. From the dorsal aspect (fig. 1) one sees the brain shining through the skin. The olfactory nerves grow out from the olfactory bulbs and reach the pigmented nasal grooves. Nerves, vessels, and muscles are visible through the transparent skin. The pigmentation is well developed ; its distribution is the same as in Pl. 39. fig. 7. The large pigment-cells of the skin are clearly pictured, also the little black spots in the membranes of the brain and of the labyrinth, lying very close together and seen through the skin.

The well developed coils of the gut are visible in the side view.

The limbs are differentiated into leg and foot. The anterior one is covered by a thin membrane, and is bent at the elbow-joint.

PLATE 39. FIGS. 8 & 8 *a*.

The larva represented in fig. 8 has a length of 35 mm. and like that of fig. 7 shows the features of a fully developed tadpole ; the characteristic peculiarities are still more accentuated. The pigment-cells of this larva are contracted into little black spots ; their distribution is as usual.

The tentacles have grown to double the length compared with fig. 7 ; in this specimen they bear no branches.

The extremities are longer and more differentiated ; they are divided into hand (or foot) and arm (or leg). The anterior one is not yet free.

No other difference of importance is to be remarked.

PLATE 39. FIGS. 9 & 9 *a*.

The tadpole measures 40 mm. in length. The differences between this larva and the specimen shown in fig. 8 are confined to the tentacles and the extremities. Note also the open spiracle, and the sense-organs in the skin over the gut.

The tentacles show several branches. The extremities are further developed, especially the posterior one. The rays of the digits are visible in the foot, and the knee-joint in the leg. The anterior limb, covered by the skin, is much smaller than the posterior; it is a curved appendage of the trunk with small digits.

PLATE 39. FIGS. 10 & 10 *a*.

The larva represented in fig. 10 is remarkably small; it measures only 32 mm. in length. It differs from fig. 9 only in the development of the extremities.

The head is still broad and flattened (fig. 10 *a*).

The hind leg has become longer and projects beyond the margin of the fin-fold. The knee is very clearly to be seen, and its joint is bent, as shown in fig. 10 *a*. The toes are well differentiated. The arm is bent at the elbow-joint, but not yet free.

PLATE 39. FIGS. 11 & 11 *a*.

The larva of fig. 10 is a well developed tadpole; that of fig. 11 is in course of metamorphosis to the frog.

Head and body are transformed in shape. The head is no longer flattened, but rounded. It is higher dorso-ventrally and narrower from right to left, but still relatively broader than in the adult frog. The mouth lies on the lower side of the head, no longer on the upper side. At its edges are the tentacles, now somewhat reduced—short threads with little branches. The spiracles are not yet closed.

The caudal portion of the body is broader—a result of the development of the legs.

The sense-organs are conspicuous, not only over the gut but also on the back of head and body (fig. 11 *a*). The skin loses its transparency and assumes the adult character.

The tail is very long and shows no sign of degeneration. The fin-fold is still well developed, in the tail itself and also in front of the cloaca.

The extremities are further developed. The anterior one is free, with elbow and fingers, the posterior is very long. The toes are united by a swimming membrane; the claws of the first three toes have begun to develop.

PLATE 39. FIGS. 12 & 12 *a*.

Fig. 12 represents a little frog with a long tail.

Head and body are still rounded, especially the snout. The mouth is shifted

still further ventrally. The tentacles are atrophied to short black stumps at the edges of the mouth.

The spiracle is still open. It lies under the insertion of the arm.

The fin-fold of the tail is shorter ; it has almost disappeared between the body and the anus.

The leg is a powerful swimming-organ with large toes, three of which bear horny claws. The anterior extremity is bent in the definitive position.

PLATE 38. FIG. 1.

Fig. 1 of Pl. 38 shows from the dorsal side a frog in a more advanced stage of metamorphosis. It is fully developed, but has still a tail, now atrophied to a short appendage.

The snout, the nostrils, and the eyes are like those of an adult frog.

I could not observe the closure of the spiracle, because neither the actual specimen nor any other of the same stage was found in the material.

The skin has made an advance : one sees a new pigmentation, dark spots on a light ground. The lateral line sense-organs are visible.

PLATE 39. FIG. 13.

Fig. 13 represents a young frog from the dorsal side.

The external features are in all respects those of a frog, the metamorphosis being now completed. The frog has its definitive coloration and sense-organs.

The tentacles have entirely disappeared. Only a small white spot with a few pigmented cells on the edge of the upper jaw of the broad crescentic mouth shows the place from which the tentacles projected in the tadpole.

Beneath the eye a short tentacle has developed.

The three claws of the toes are well developed. A fourth has grown out at the basis of the first toe.

The frog grows still further, but does not change in shape and appearance.

PLATE 38. FIG. 2.

The anterior half of a fully developed adult frog is shown in fig. 2 from the right side.

The artist has represented the mottled skin with the lateral sense-organs in colour.

The nostrils are prominent, as also the large eyes with the brown iris. The tentacle under the eye is very short and thin. The mouth is situated on the ventral side of the snout.

The short feeble arms bear four fingers without claws.

On surveying the whole development of the external features of *Xenopus* and comparing it with that of a species of *Rana*, we perceive that we have to deal with a very remarkable form.

The peculiarities of the *Xenopus* larva are often referred to : I propose to put them together once more with reference to the figures.

Naturally the peculiarities are correlated with the mode of life of the larva, especially with the feeding habits. Bles describes in an interesting manner how the food, consisting of little planktonic organisms such as *Chlamydomonas*, is carried in with the stream of water and filtered off in the gill-chamber. This explains the absence of horny teeth and the persistence of the opercular opening.

The shape of the larva is extraordinary, and is reminiscent of that of fishes. The long tail with the broad fin-fold which occupies two-thirds of the length of the whole animal is hardly to be found in any other tadpole. The broad flat head is very characteristic, especially the long tentacles which project at the edges of the mouth. These tentacles, along with the fish-like body, have led some authors to compare the *Xenopus* larva with a Siluroid form.

As already said, we find no horny teeth in the mouth at any stage in the *Xenopus* larva. All the tadpoles of *Rana* bear these teeth for rasping the flesh etc.

The development of the gills is remarkable too. There are three external gills which remain rudimentary : at the height of their development they are only short simple threads. I have never seen bifurcation nor branches. They evidently exist but a short time, and are soon grown over by the operculum.

There are no internal gills at all : where they would normally be situated filter-processes are developed for filtering the water entering through the mouth. Small organisms are held back in the gill-chamber and the water leaves the body through the spiraculum. For this reason the spiraculum is still open in the young frog with a long tail at the end of the metamorphosis.

Correlated with the frog's life in the water is the fact that the sense-organs of the lateral line do not atrophy at the metamorphosis, but persist as functional organs in the adult.

Bles called attention to the strange pigmentation of the larva, which is absent from special parts of body and tail, and suggested a biological explanation for this distribution.

The development of *Xenopus* is sufficiently peculiar to merit extended treatment, not only as regards the external features but also the internal organs. The latter portion of the task I intend either to undertake myself or to entrust to one of my assistants.

nasal pit

tentacle

olfactory nerve

eye

optic nerve

gill chamber

epiphysis

aortic arches

ear

heart

pronephros

lymph heart

gut

Fig. 1.

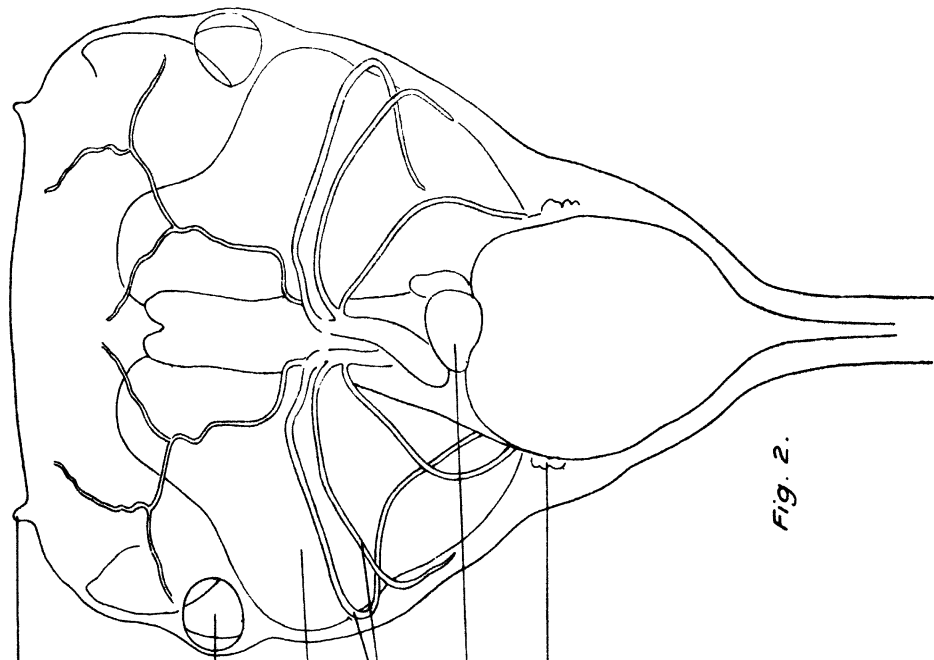
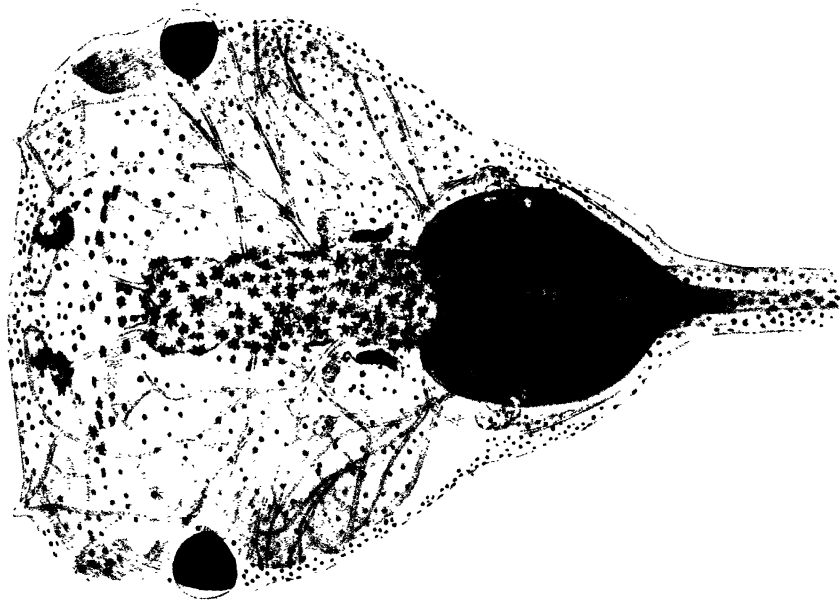


Fig. 2.



Peter

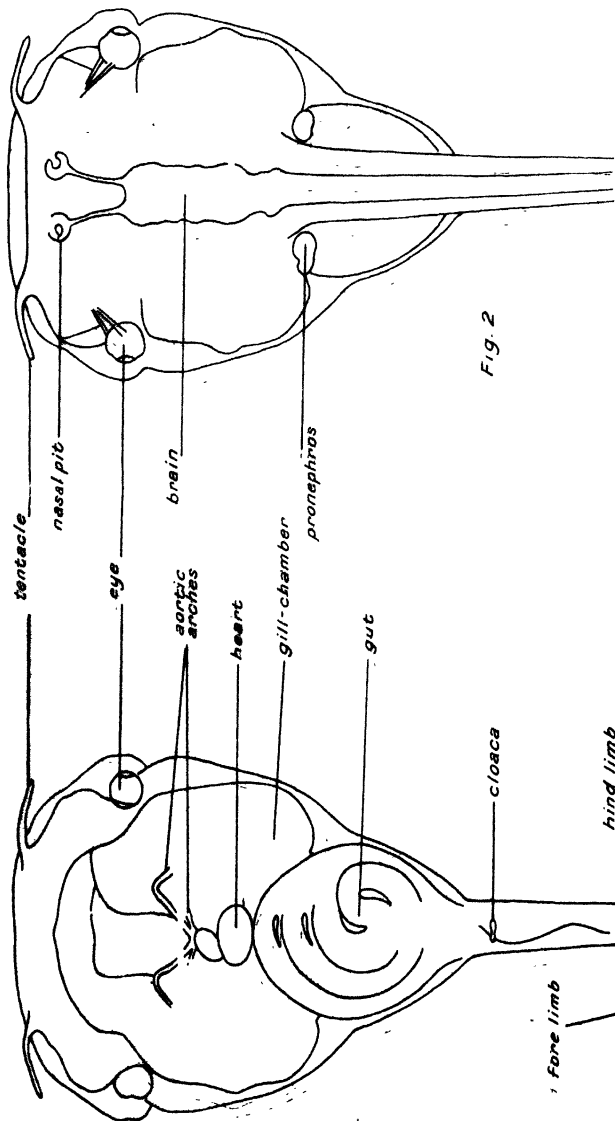
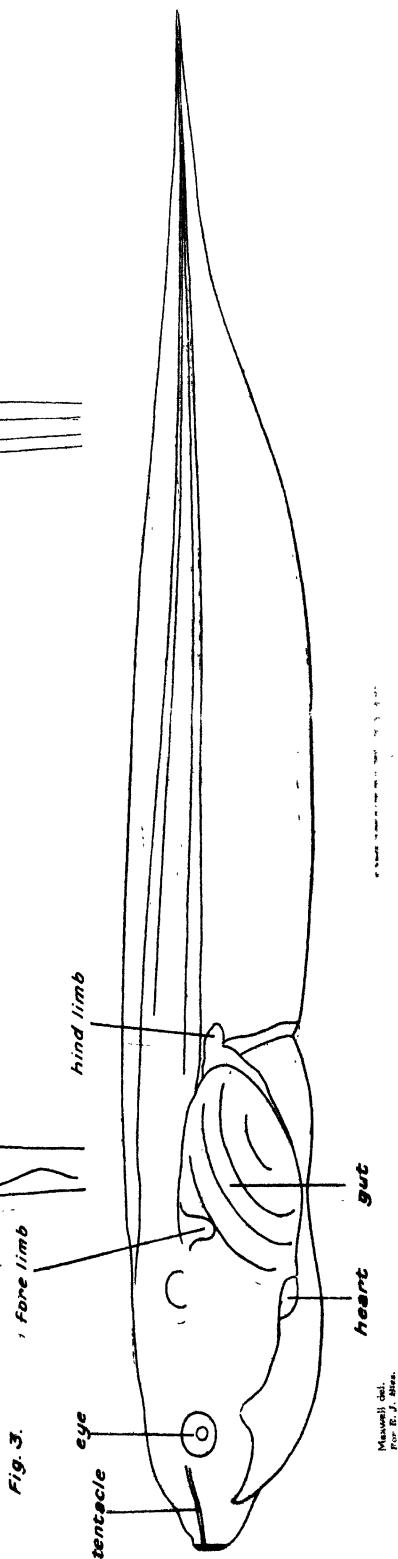


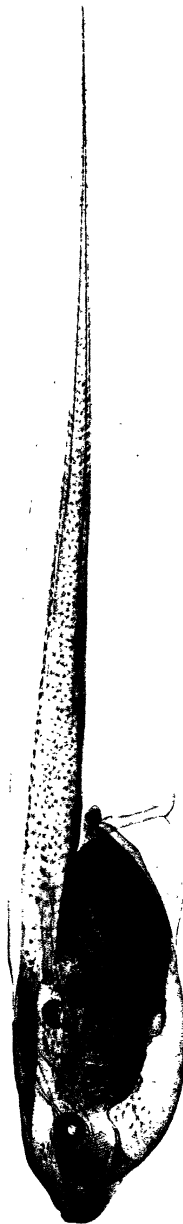
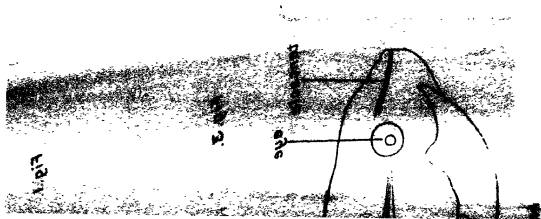
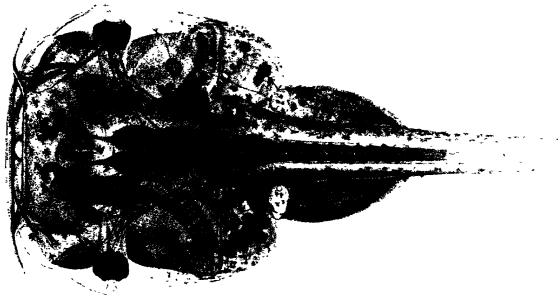
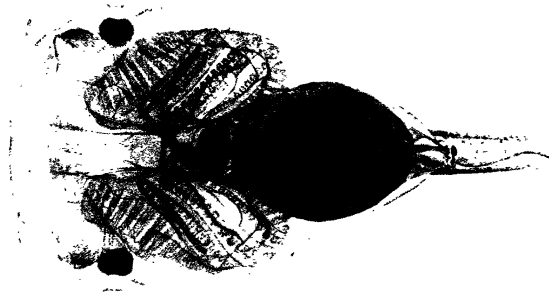
Fig. 2



Maxwell del.
Rev. E. J. Allen.

Peter.

JOURN. LINN. SOC. ZOOL., VOL. XXXVII, PL. 35



Manwell del.
For L. J. Allen

XENOPUS LAEVIS

Wardlaw 6.5mm 1.1x1

Peter.

ch

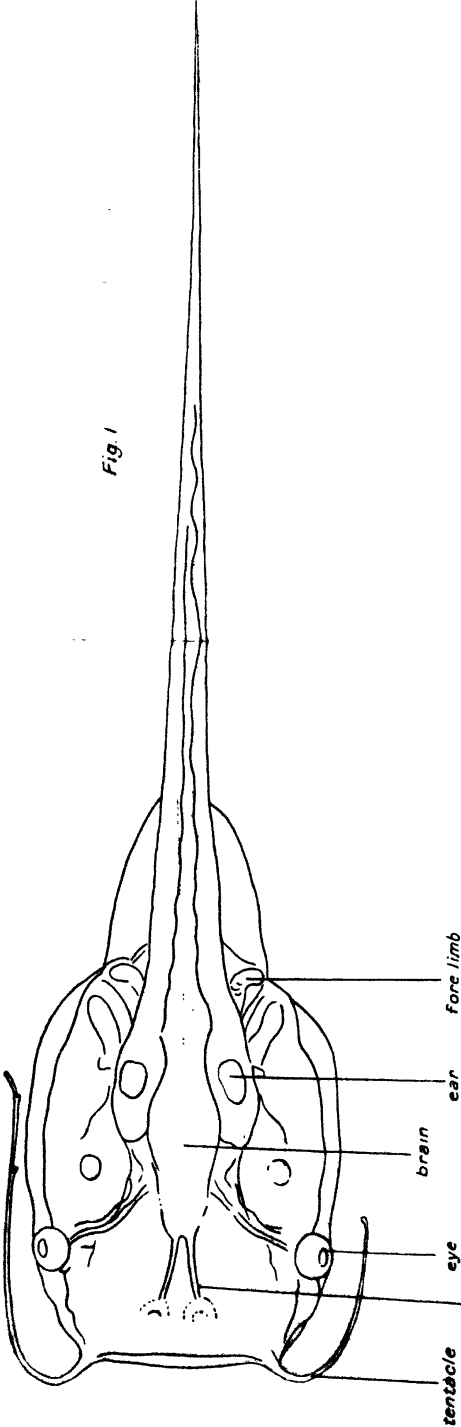


Fig. 1

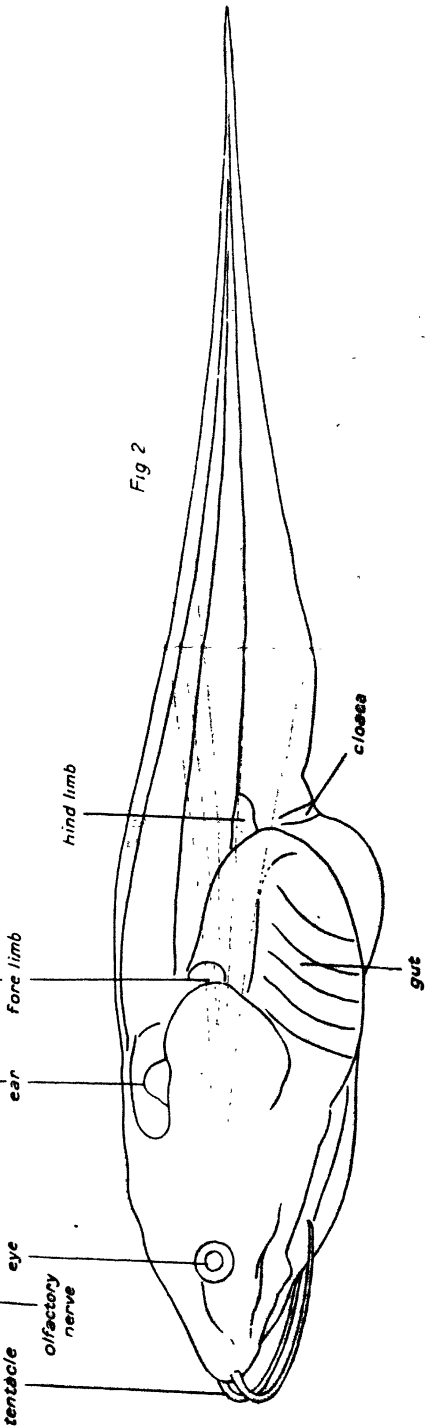
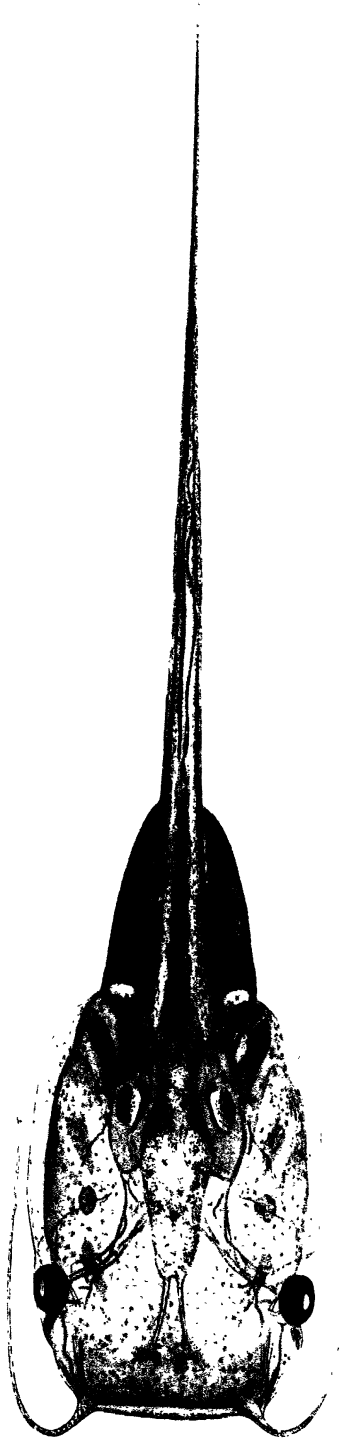


Fig. 2



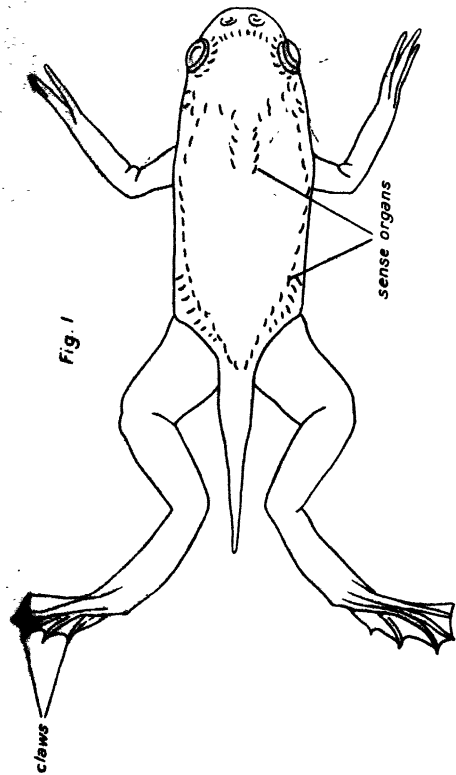


Fig. 1

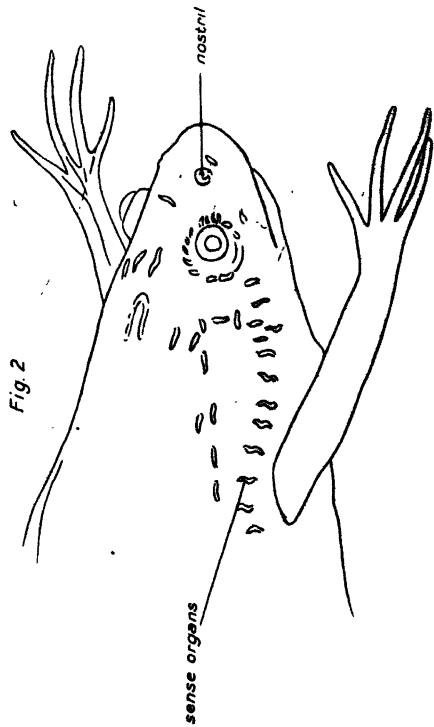


Fig. 2

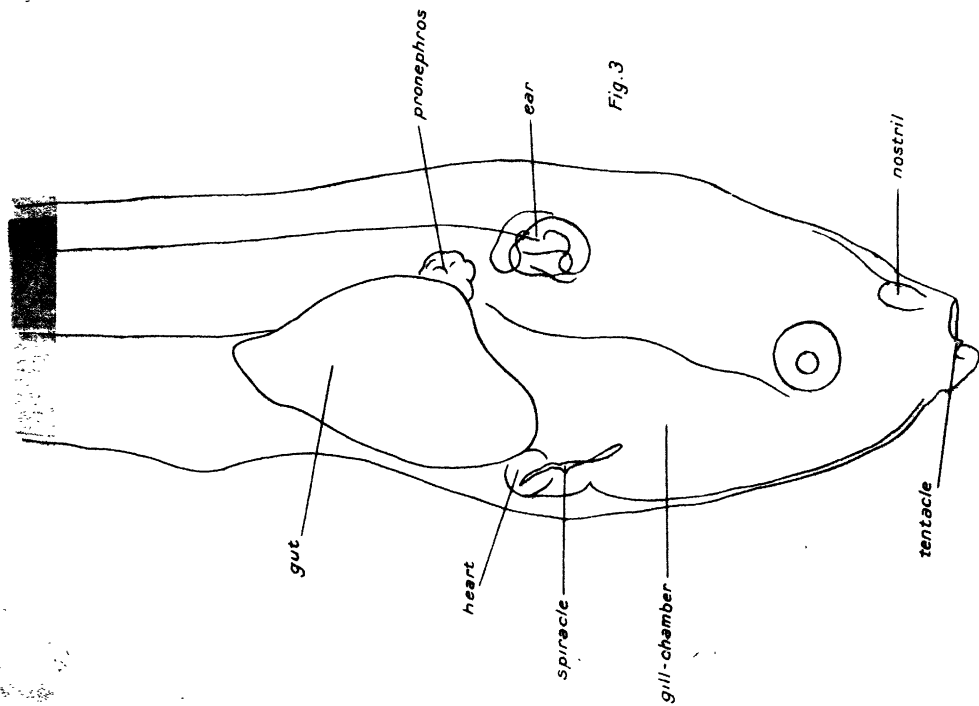
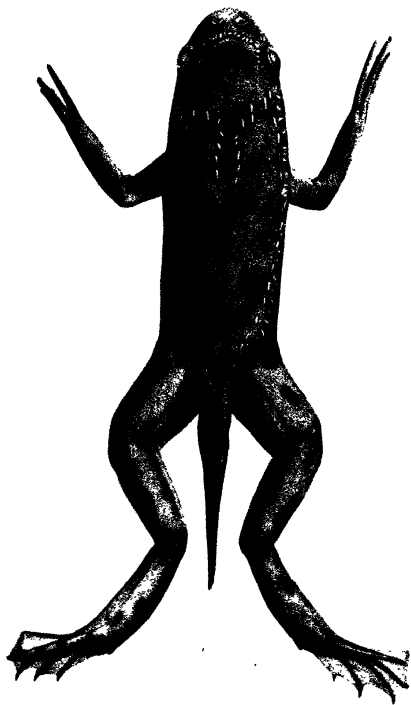


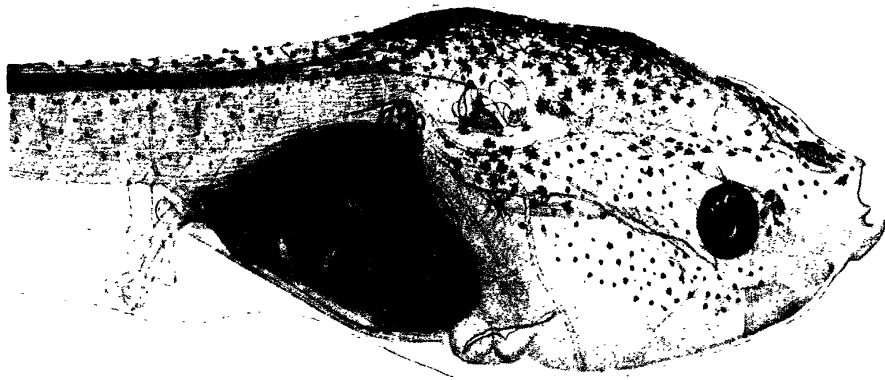
Fig. 3

Peter.



Maxwell del.
Peter Sc. J. Steen

XENOPUS LAEIS.



Brachyura from the Coasts of China.

By ISABELLA GORDON, D.Sc., Ph.D.

(With 36 Text-figures.)

[Read 6th November, 1930.]

INTRODUCTION.

The material with which the present paper deals consists of (1) a small collection of Decapoda, chiefly Brachyura, from Amoy and Poi-tai-ho, sent for identification by C. J. Shen, Esq., of the Fau Memorial Institute of Biology, Peking; (2) a much larger collection from Hongkong, presented to the British Museum by R. W. D. Barney, Esq.; (3) several specimens from Chufoo*, Shantung, presented by Dr. E. Huddle.

The majority of the species are well known and, for literature dealing with these as well as information regarding synonymy and distribution, the following works will be found most useful:—(a) Alcock, various papers in J. Asiatic Soc. Beng. vols. lxiv., lxv., lxvii.-lxix., 1895-1900; (b) Parisi, a series of papers in Atti Soc. ital. Milano, vols. liii.-lvii., 1914-1918, and (c) Balss, several papers in Arch. Natg. Berlin, vols. lxxxviii.-xc., 1922-1924.

Mr. Barney had identified many of the species in his collection, only new or little-known species are dealt with very briefly in the succeeding pages, and the author is entirely responsible for all descriptions and figures as well as for the determination of all new and most of the other species described.

The male abdominal appendages have been studied in considerable detail, because, although hitherto overlooked by most carcinologists, it is probable that they may prove to be of considerable systematic importance in many Brachyura. For example, these appendages afford a ready and reliable means of distinguishing males of (1) the three species of Xanthidae compared on pp. 543-545; (2) closely allied species of Portunidae (text-figs. 10, 12, & 13); and (3) the three species of the genus *Paracleistostoma* (text-figs. 26, 27, & 28) examined.

Leaving aside the genus *Pilumnus*, no two species of the Xanthidae examined had identical anterior male appendages, although the differences can sometimes be observed only under the microscope after the appendages have been removed from the specimens. The two species of (a) *Atergatis* and (b) *Halimede*† differ considerably from each other as regards these appendages, but it has not

* These localities are denoted by the letter A., P., H., and C. in the list of species, pp. 526-529.

† See list of species, p. 528.

been deemed advisable to include figures for all the Xanthid species in the present paper.

As regards the second pair of male abdominal appendages, the species of Xanthidae in the Chinese collections fall into two groups. In the first group, the larger by far, these appendages are short, measuring only one-fifth to one-third the length of the anterior pair (text-fig. 22 C, 2). In the second group (e. g., in *Menippe convexa* Rathbun, *Epixanthus frontalis* (A. M.-Edw.), and *Eriphia larimana* var. *smithi* McLeay), these appendages exceed the anterior pair in length, and may be bent back upon themselves distally. Whether or not this difference is of systematic importance could be determined only after a revision of the whole group. I hope to be able to look into this question at some future date.

Several species referred to the genus *Pilumnus* have the anterior male appendages either of the type represented in text-fig. 17 a (without a large spine under the beak-like apex) or that illustrated in text-figs. 16 c and 18 b (with a very large spine under the apex). The fact that both these types occur also in the genus *Lilocheira* (text-fig. 25 A & B) suggests a much closer relationship between these genera than has hitherto been admitted. Authors are agreed that there is a close resemblance between certain Xanthids and certain of the Gonoplacidae; it is not always easy to detect, in small species, whether or not the male genital duct passes forward along a shallow depression in the sternum. In any revision of these allied Cyclometopa and Catometopa a careful study of the male appendages might be of considerable help.

The author is indebted to Dr. B. Parisi of the Museo di Storia Naturale, Milan, to Prof. A. Schellenberg of the Zoologisches Museum, Berlin, and to the authorities of the Strasbourg and Lübeck Museums for sending material on loan or in exchange.

List of Species represented.

ANOMURA.

GALATHEIDEA.

- Petrolisthes lamarcki* * (Leach). H.
- Porcellana ornata* Stimpson. H.
- „ *pulchra* Stimpson. P.
- „ *serratifrons* Stimpson. P., A
- „ *spinulifrons* Miers. H.
- Raphidopus ciliatus* Stimpson.

BRACHYURA.

1. DROMIACEA.

- Dromia dehaani* † Rathbun. H.
- Petalomera granulata* Stimpson. H.

* *P. "speciosus"* Stimpson—see Parisi, 1917, p. 7.

† Rathbun, 1923, p. 68.

2. OXYSTOMATA.

- Dorippe dorsipes* (Linn.). H.
 „ *facchino* (Herbst). H.
 „ *japonica* v. Siebold. H.
Mursia armata de Haan. H.
Matuta planipes Fabr. (— *M. lunaris* Alcock). P., H.
 „ *victor* of authors (— *M. lunaris* (Forskål) Balss). H., C.
Myra fugax (Fabr.). H.
Philyra tuberculosa Stimpson. H., P.
Leucosia unidentata de Haan *. H.
 „ *rhomboidalis* de Haan (— *L. maculata* Stimpson). H.
Ixoides cornutus (?) MacGillchrist. H.
Pariphiculus mariannae (Herklots) †. H.
Arcania quinquespinosa Wood-Mason. H.
 „ *septemspinosa* (Fabr.). H.
 „ *undecimspinosa* de Haan. H.
Lyrculus politus Parisi. H.

3. BRACHYRRHYNCHA.

a. CYCLOMETOPA.

- Lissocarcinus arkati* Kemp. H.
Neptunus (*Neptunus*) *sanguinolentus* (Herbst). H.
 „ (*Amphitrite*) *argentatus* (White). H.
 „ (*Hellenus*) *hastatorides* (Fabr.). H.
 „ „ *pulchricristatus*, nom. nov. H.
 „ „ *tuberculatus* A. M.-Edw. H.
 „ (*Lupocyeloporus*) *gracilimanus* (Stimpson). H.
Charybdis (*Goniobellinus*) *sinensis*, sp. n. H.
 „ „ *truncatus* (Fabr.). H.
 „ (*Goniosoma*) *anisodon* de Haan. H.
 „ „ *barneyi*, sp. n. H.
 „ „ *merguensis* de Man. H.
 „ „ *miles* de Haan. H.
 „ „ *variegata* (de Haan). H.
Thalamita crenata Latr. H.
 „ *sima* A. M.-Edw. H.
Stylla serrata (Forsk.). H.
Kraussia integra (de Haan). H.
Cancer pygmaeus Ortmann. P.
Menippe convexa Rathbun (— *M. ortmanni* de Man). H.
Pilumnus laevimanus Dana. H.
 „ *penicillatus*, sp. n. H.
 „ *seminudus* Miers. H.
 „ *sinensis*, sp. n. H.
Actumnus setifer (de Haan). H.
Galene bispinosa (Herbst). H.
Actæa amoyensis (de Man). A.
 „ *helleri* (?) A. M.-Edw. H.

* *L. obtusifrons unidentata* Balss, 1922, Arch. Naturg. A. 3, p. 128.

† Nobili, 1906, Ann. Sci. nat. (9) iv. p. 165, footnote.

- Actæa nodulosa* White. H.
 „ *savignyi* var. *pura* Stimpson. H.
Atergatis integerrimus (Lam.). H.
 „ *reticulatus* (de Haan). H.
Medæus granulatus Haswell. H.
Xantho cruratus (M.-Edw.). H., P.
 „ *distinguendus* (de Haan). H., P.
Halimede ochtodes (Herbst). H.
 „ *tyche* (Herbst). H.
Liagore rubromaculata de Haan. H.
Etisus lavimanus Randall. H.
Epixanthus frontalis (A. M.-Edw.). H.
Eriphia lavimana var. *smithi* McLeay. H.
Parathelphusa sinensis (A. M.-Edw.). H., A.

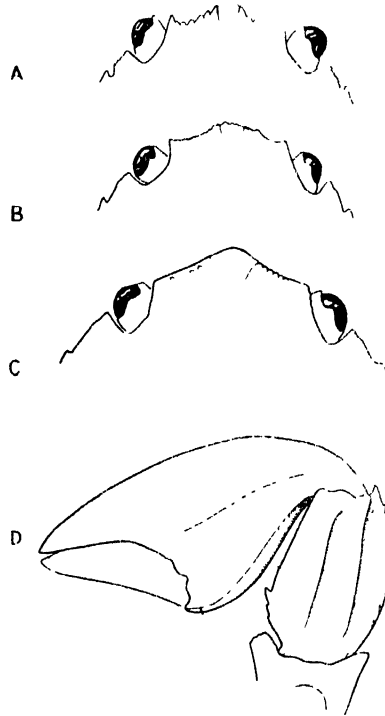
b. CATOMETOPA.

- Scolopidia spinosipes* Stimpson. H.
Uca arcuata (de Haan). A.
 „ *garnardi* H. M.-Edw. (= ? *U. splendida* Stimpson). H.
 „ *lactea* (de Haan). H.
 „ *mani* Rathbun (= *U. acutus* de Man). H.
 „ *marionis* var. *nitidus* Dana. H.
Ocypoda ceratophthalma (Pallas). H.
Eucrate crenata de Haan. A., H.
 „ *dentata* (Stimpson). H.
 „ *sulcatifrons* (Stimpson). H.
 „ *transversus* (Stimpson). H.
Carcinoplax longimanus de Haan. H.
Latocheira amoyensis, sp. n. A.
 „ *subintegra* Lanchester. H.
Macrophthalmus convexus Stimpson. H.
 „ *latreillei* (Desm.). H.
 „ *pacificus* Dana. H.
 „ *teschi* Kemp. H.
Paraclestostoma depressum de Man. A.
Scopimera globosa de Haan. H.
Tympanomerus ceratophora (Koelbel). H.
Michtyris longicarpus Latr. H.
Grapsus strigosus Herbst. H.
Metopograpsus quadridentatus Stimpson. A., H.
Brachynotus penicillatus de Haan. A., H.
 „ *sanguineus* (de Hann). H., P.
Eriocheir sinensis M.-Edw. P.
 „ *japonicus* de Haan. H.
Gatice depressus (de Haan). A., H.
Chasmagnathus convexus de Haan. A., H.
Metaplaa elegans de Man. H.
 „ *longipes* Stimpson. A., H.
 „ *sheni*, sp. n. A.
Sesarma (*Chirromantes*) *bidens* (de Haan.). H.
 „ (*Holometopus*) *hæmatocheir* (de Haan.).
 „ (*Sesarma*) *intermedia* (de Haan.). A., H.
 „ (*Parasesarma*) *picta* (de Haan.). H.

4. OXYRHYNCHA.

Egeria arachnoides (Rumph.). H.*Doclea canalifera* (?) Stimpson (incompleto). H.„ *ovis* (Herbst). H.*Micrappa philyra* (Herbst). H.*Lambrus longimanus* Leach. H.„ *validus* de Haan. H.*Pugettia cristata*, sp. n. A.„ *quadridentis* de Haan. P.

TEXT-FIG. 1

*Porcellana ornata* Stimpson.

A-C, anterior portion of carapace of three specimens, camera lucida drawing, $\times 12.5$; D, cheliped, $\times 8.5$.

GALATHEIDEA.

PORCELLANA ORNATA Stimpson.

Stimpson, 1858, p. 242; 1907, p. 188.

Three specimens from Hongkong appear to belong to *Porcellana ornata* Stimpson; as no figures were given by that author, the cheliped and the front are now illustrated (see text-fig. 1 D and 1 A-C). The setæ on the outor

lower border of the palm had been rubbed off the chela from which the illustration was obtained; the carpus is characterised by two pronounced longitudinal ridges on the dorsal surface. The front differs somewhat in all three specimens, but is always triangular with concave sides and a marked median depression towards the apex. The areolations described by Stimpson on the anterior portion of the carapace are present in all three. In two specimens there is a single small spine a short distance behind the orbit. In the other specimen (that represented in text-fig. 1 A) there are five or six spinules on the convex portion of the lateral border immediately posterior to the antenna.

Previously recorded from Hongkong.

PORCELLANA PULCHRA Stimpson.

Stimpson, 1858, p. 243; 1907, p. 192.

This species is represented by a single specimen from Pei-tai-ho (Shen Coll.). As Stimpson's figure (1907, pl. xxii. fig. 1) is rather small, an outline of the carapace, which is very characteristic, and of the cheliped are given (text-figs. 2 & 3). Previously recorded from Hongkong.

PORCELLANA SPINULIFRONS Miers.

Miers, 1879, p. 46.

Several specimens in the Barney collection prove to be identical with the type-specimens of *P. spinulifrons* Miers. As no figures were given by that author, it has been thought advisable to give several illustrations (text-figs. 4 A-C & 5).

The species is, in many respects, similar to *P. serratifrons* Stimpson (1907, p. 189, pl. xxiii. fig. 2), and it is possible that transitional forms may yet be found. The specimens referred to Stimpson's species (see list on p. 526) have, as a rule, only a single spine on the postero-lateral border of the carapace (text-fig. 6), but occasionally other spinules are present; the lobules of the front are not so deeply separated off from each other, and the spines on the anterior margin of the carpus of the cheliped are, as a rule, less pronounced, sometimes almost obsolete. It is just possible that *P. spinulifrons* is a young, though sexually mature (larger ♀ ovigerous), form of *P. serratifrons*.

Previously recorded from Korea and Japan.

OXYSTOMATA.

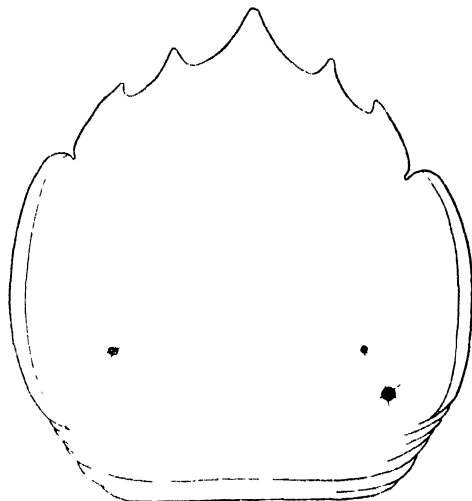
IXOIDES CORNUTUS (?) MacGilchrist.

MacGilchrist, 1905, p. 255; pl. lxxiii, figs. 2-2 b, Ill. Zool. 'Investigator,' Crustacea (referred to under Alcock and others, 1892-1908; Ihle, 1918, p. 314).

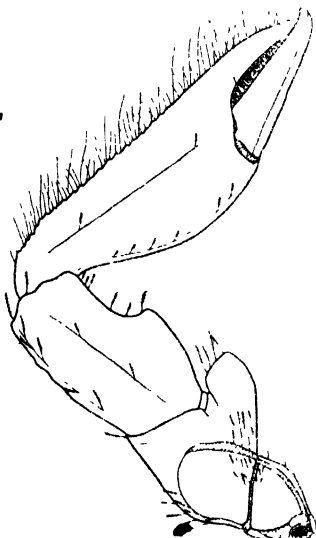
This genus is known only from the three ♂♂ of *I. cornutus* described by MacGilchrist from the Persian Gulf. In the Barney collection are three specimens (2 ♂♂ 53×30 mm.* and 52.8×26.4 mm.; 1 ovigerous ♀, damaged)

* The length of carapace does not include the stout posterior processes, but the breadth includes the lateral processes.

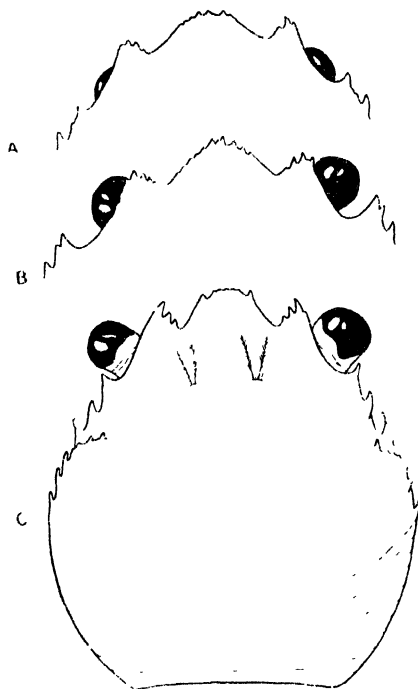
TEXT-FIG. 2



TEXT-FIG. 3.



TEXT-FIG. 4.



TEXT FIG. 5.

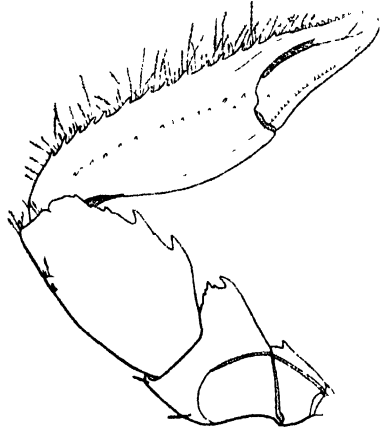


Fig. 2.—*Porcellana pulchra* Stimpson, carapace in dorsal aspect, $\times 12.5$.

Fig. 3.—*Porcellana pulchra* Stimpson, cheliped, $\times 12.5$.

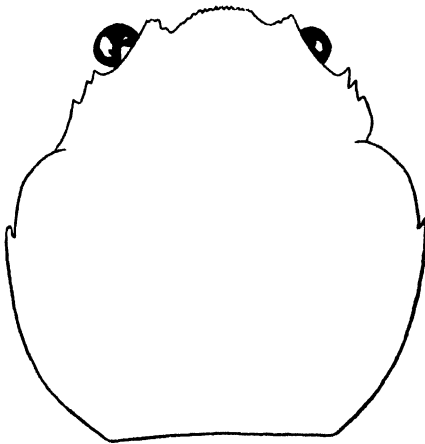
Fig. 4.—*Porcellana spinulifrons* Miers. A & B, anterior portion of carapace of type-specimens; C, carapace of a specimen from Hongkong. $\times 15$.

Fig. 5.—*Porcellana spinulifrons* Miers, cheliped, $\times 8.5$.

which undoubtedly belong to this genus, but, owing to the fact that all are incomplete, their identity with MacGilchrist's species is by no means certain. The lateral processes are shorter than in *I. cornutus*, being only about one-fifth instead of one-fourth of the total length. In the male specimens they are slightly inclined forwards and end in a blunt rounded tip. In *I. cornutus*, on the other hand, they project straight outwards, and taper away to an acute point. The first abdominal appendage is long and straight, with apex as represented in text-fig. 7. Only the arm of the cheliped remains.

The only known ♀ of the genus is very incomplete, the left lateral process tapers abruptly towards the apex which is acute; that on the right side is

TEXT-FIG. 6.



TEXT-FIG. 7.

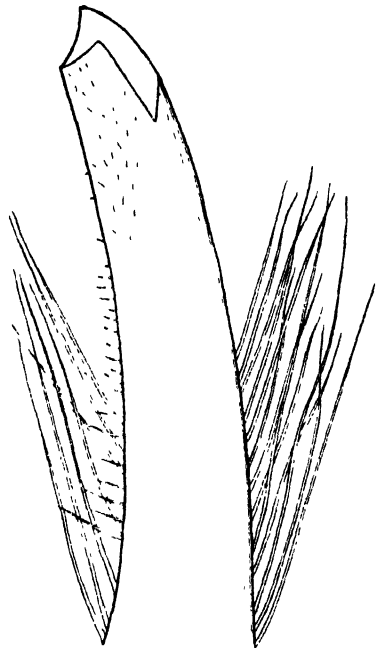


Fig. 6.—*Porcellana serratifrons* Stimpson, carapace in dorsal aspect, $\times 8.5$.

Fig. 7.—*Ixoides cornutus* ? MacGilchrist, apex of anterior ♂ abdominal appendage, $\times 45$.

wanting. The left cheliped is complete, save for the digits; the palm is somewhat longer and narrower than in *I. cornutus* (Ill. Zool. 'Investigator,' pl. lxxiii. fig. 2 b). The abdomen has five segments, but the first of these would, in all probability, be concealed by the carapace.

LYREIDUS POLITUS Parisi.

Parisi, 1914, p. 34, pl. xiii, fig. 5.

Material.—3 ♂♂ measuring 29.4×15.5 – 34.8×18.5 mm.; 1 ♀ measuring 37×19.5 mm. from Hongkong.

This is only the second occurrence of the species; the type-specimen (♂) was recorded from Enoshima, Japan.

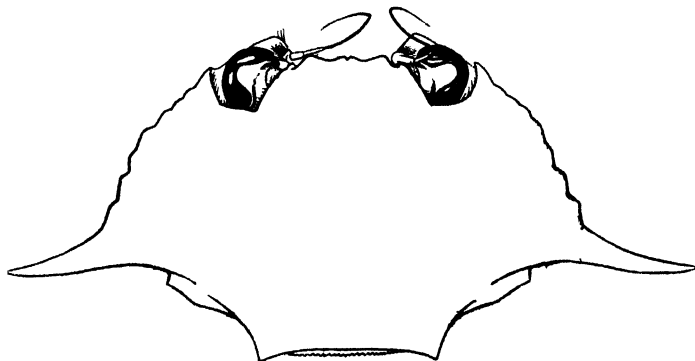
CYCLOMETOPA.

LISSOCARCINUS ARKATI Kemp.

Kemp, 1923, pp. 405-408, pl. x, fig. 1.

A single ovigerous ♀ from Hongkong agrees in all points with the description and figure given by Kemp, save that (1) the transverse setose ridges are restricted to the anterior portion of the carapace and (2) the posterior is equal to the

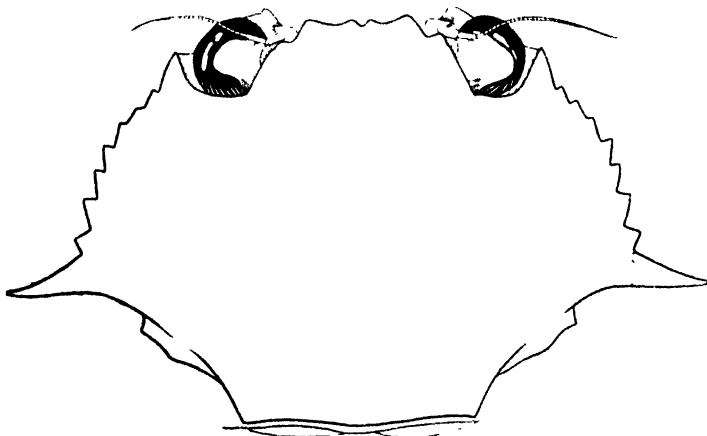
TEXT-FIG. 8.



Neptunus (Hellenus) pulchricristatus, nom. nov., carapace in dorsal aspect, $\times 4$.

fronto-orbital border. In the former respect it resembles *L. boholensis* Semper, but, as Kemp has pointed out, it differs in several important respects from the latter species as described by Rathbun (1910, p. 363).

TEXT-FIG. 9.



Neptunus (Hellenus) spinipes Miers, carapace of co-type in dorsal aspect, $\times 4.5$.

The measurements (in mm.) of the specimen are as follows:—length of carapace=17.5; breadth of carapace=21.5; fronto-orbital breadth=14.5; breadth of front excluding inner orbital angles=7.1.

Previously recorded from off the mouth of the River Hughli.

NEPTUNUS (HELLENUS) PULCHRICRISTATUS*, nom. nov.

(= *Neptunus spinipes* Alcock, 1899, pp. 31-32, 39-40, nec Miers, 1886, p. 178, pl. xv, fig. 1.)

Material.—5 ♂♂ measuring 27×11.7 – 32×12.8 mm.; three ♀♀ measuring 24.9×10.6 – 27×11.8 mm. (2 ovigerous).

Description.—According to Alcock's key (1899, pp. 31-32), these specimens belong to the species *N. (Hellenus) spinipes* Miers (1886). On comparing them with the type-specimens, however, they were found to differ from these in several important respects:—(1) The angle formed by the junction of the posterior with the postero-lateral border of the carapace is distinctly more spiniform (*cf.* text-figs. 8 & 9). (2) The first eight teeth of the antero-lateral border are merely blunt lobes, the first three of which are almost obsolete; in *N. spinipes* they are much more pronounced and acute. (3) The lateral epibranchial spine is much longer than in the 'Challenger' specimens, so that the total breadth—from tip to tip of spines—is 2.3–2.5 times as against 1.7–1.85 times the length of the carapace. (4) Both species have a crest on the second and on the third abdominal segments in both sexes; in the Hongkong specimens both crests are "elegantly beaded," whereas in *N. spinipes* the crests are more prominent, but, while that on segment 2 is faintly beaded, that on segment 3 is smooth and markedly bilobed. (5) The abdominal appendages in the ♂ are also rather different in the two species (*cf.* text-figs. 10 A & 10 B).

These specimens are undoubtedly the same as Alcock's material (1899, pp. 39-40). This author remarks that "the specimens figured by Miers has abnormally short lateral epibranchial spines," but all Miers's three co-types have similar short spines.

Previously recorded from Madras, Andamans, Gulf of Martaban, Arakan Coast, and Muscat.

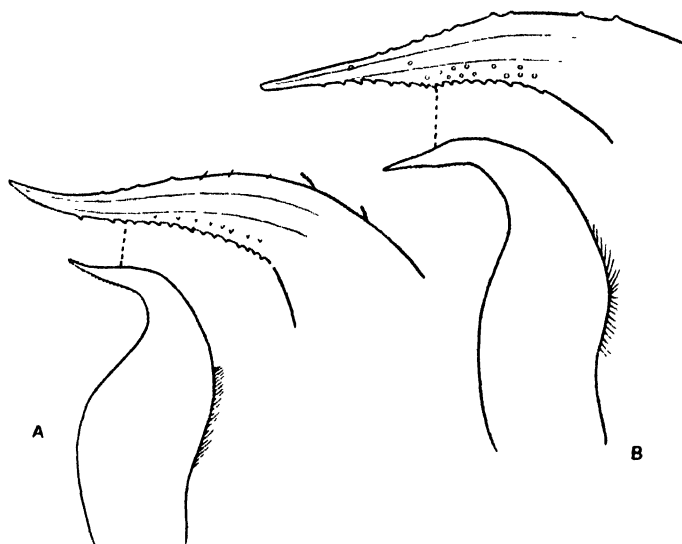
CHARYBDIS (GONIOHELLENUS) SINENSIS, sp. n.

Material.—1 ♂, 22.7×13.8 mm. (holotype); 2 ♀♀, 20.7×12.3 and 26×15.5 mm., the latter ovigerous from Hongkong.

Description.—According to Alcock's key (1899, pp. 48-51), these specimens would be identified as *G. hoplites* Wood-Mason. On comparing the Chinese specimens with a ♂ and a ♀ specimen of that species in the British Museum Collection the ♂ especially proved to be different. In *G. hoplites* the sixth abdominal segment is of the form represented in text-fig. 12 a, truncate triangular, whereas in the Chinese specimens (text-fig. 12 c) that segment is broadest in the centre and each lateral border is convex. The first pair of abdominal appendages differ markedly as illustrated in text-fig. 12, b, b' and d, d'. There are other minor differences:—(1) In *G. hoplites* the teeth on the lateral margin are more conspicuously serrated along the posterior margin and "are square-cut lobules separated by wide and deep notches" (Alcock and Anderson, Ill. Zool. 'Investigator,' Crust. pl. xxiii, fig. 6; Alcock,

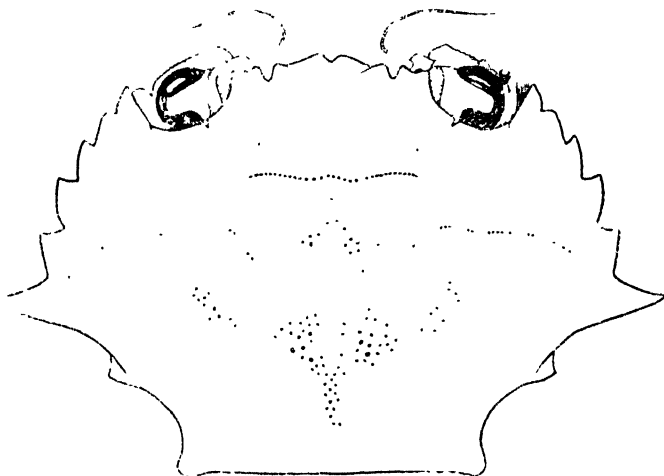
* This species was described under the name of *N. (H.) alcocki* in a preliminary note (Ann. & Mag. Nat. Hist. (10) vi, p. 521, 1930), but that name is preoccupied.

TEXT-FIG. 10.



Anterior ♂ abdominal appendage of (A) *Neptunus (Hellenus) pulchricristatus*, nom. nov., and (B) *N. (H.) spinipes* Miers. $\times 15$ and 45 .

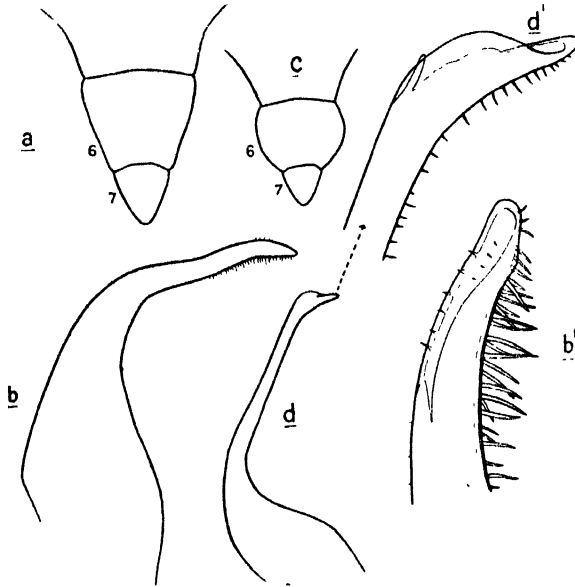
TEXT-FIG. 11.



Charybdis (Goniohellenus) sinensis, sp. n., carapace in dorsal aspect, $\times 4.5$.

1899, p. 66); compare with text-fig. 11. (2) The scale-like granulations on the palm of the chela are more highly developed in *G. hoplites*, and (3) the lobulations on the carapace are much more pronounced. While most of these differences might be due to the marked difference in size of the specimens (*G. hoplites* ♂ measures 42.5×21.7 mm.; ♀ 30.5×16.4 mm.), those illustrated in text-fig. 12 *a-d* are certainly not such as can be explained away thus.

TEXT-FIG. 12.



a, segments 6 and 7 of ♂ abdomen ($\times 4$); *b*, anterior ♂ abdominal appendage ($\times 9$), and *b'*, apex of same enlarged ($\times 36$) of *Charybdis (Goniosoma) hoplites* Wood-Mason; *c*, *d*, & *d'*, ♂ abdominal segments 6 and 7 and anterior ♂ abdominal appendage of *Ch. (G.) sinensis*, sp. n., at same magnifications.

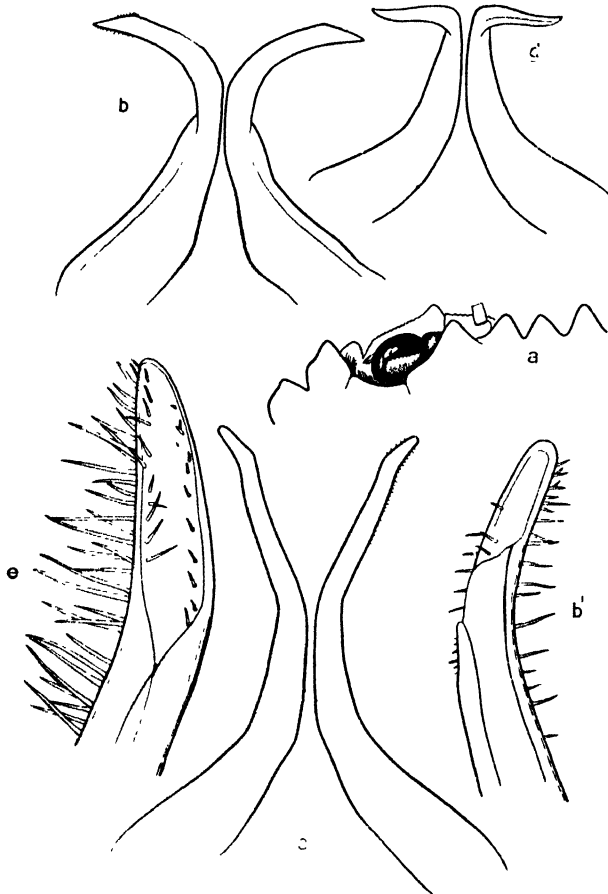
CHARYBDIS (GONIOSOMA) BARNEYI, sp. n.

Material.—2 ♂♂, measuring 50×32 mm. (holotype) and 43×28.4 mm., respectively.

Description.—A *Goniosoma* with no transverse ridges on the carapace behind the level of the last lateral spine and with not more than three large spines on the anterior border of the arm (Alcock, 1899, p. 49, group A 1). External orbital spine (text-fig. 13 *a*) rather blunt and slightly notched; second spine also notched, though to a lesser extent in the holotype; succeeding spines acute. Carapace pubescent. Chelipeds just over twice the length of the carapace, smooth, save for the usual spines; six low costæ (one of which is on the inner surface) on the palm; three more or less distinct ridges on the outer surface of the wrist; two or three spines on anterior border of arm, one spine and three spinules on wrist, four spines and one spinule on palm.

Sixth abdominal segment with sides parallel for about two-thirds of their length, then rapidly converging. Anterior pair of abdominal appendages as illustrated in text-fig. 13 *b* and *b'*. Merus of last pair of thoracic appendages 1.5 times as long as broad, armed with a spine near the distal end of the posterior border.

TEXT-FIG. 13.



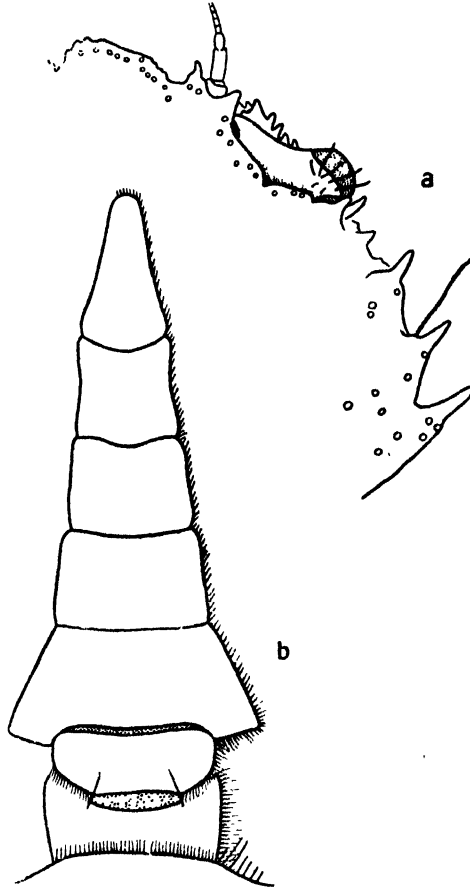
a, part of antero-lateral border and front of *Charybdis* (*Goniosoma*) *barneyi*, sp. n.; *b*, anterior ♂ abdominal appendages of same species; *b'*, apex of one of these enlarged; *c*, anterior ♂ abdominal appendages of *Ch. (G.) rivers-andersoni* Alcock; *d*, same of *Ch. (G.) annulata* (Fabr.); *e*, apex of one of these in *Ch. (G.) crucifera* (Fabr.). (*a*, *b*, *c*, & *d*, $\times 7$; *b'* & *e*, $\times 37$.)

Remarks.—In the British Museum Collection are specimens, presented by the Indian Museum, of all the species of *Goniosoma* mentioned by Alcock (1899, p. 49) in group A.1 of his key. The Chinese specimens, however, do not agree with any of these, nor with specimens that appear to belong to *Charybdis*

(*Goniosoma*) *japonica*, A. M.-Edw. All these species, with the exception of *Ch. (G.) annulata* (Fabr.), have straight ♂ abdominal appendages somewhat after the type represented in text-fig. 13 c. In *Ch. (G.) annulata* (text-fig. 13 d) the bending is more abrupt and occurs nearer the apex than in *Ch. (G.) barneyi*.

This species appears to be most nearly related to *Ch. (G.) crucifera* (Fabr.) and *Ch. (G.) rivers-andersoni* Alcock. It differs from the former in having

TEXT-FIG. 14.



Pilumnus sinensis, sp. n.

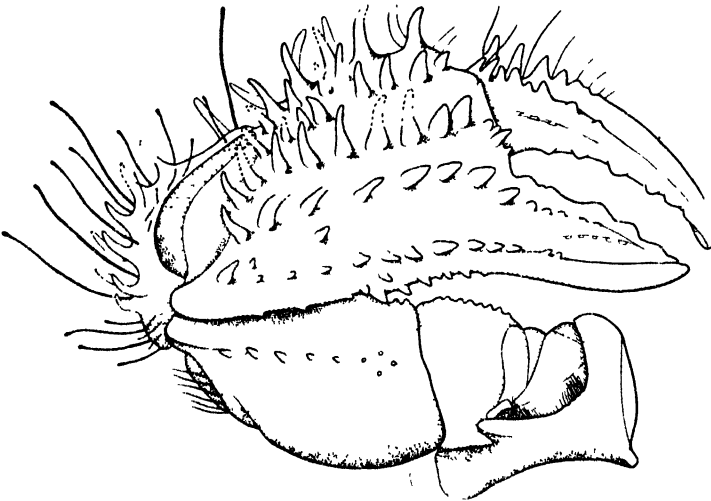
a, part of front and antero-lateral border of holotype, $\times 4.5$; b, ♂ abdomen, $\times 3$.

(1) the outer orbital spine less truncated anteriorly; (2) the sides of the sixth ♂ abdominal segment convergent only in the distal third of their length; (3) the ♂ abdominal appendages also differ (*cf.* text-figs. 13 b' and 13 e). From *Ch. (G.) rivers-andersoni* it differs in having (1) the spines on the lateral border as well as all the spinous lobes of the front less acute; (2) less prominent

spines on the chelipeds and a more inflated palm ; (3) the inner notch or fissure on the upper orbital border almost obsolete, merely indicated by a faint linear depression (in *Ch. (G.) rivers-andersoni* there is a conspicuous fissure) ; and (4) more curved ♂ abdominal appendages (cf. text-fig. 13 *b* & *c*). It also differs from both in having three instead of two longitudinal sulci on the outer surface of the palm.

Ch. (G.) barneyi may prove to be identical with the *Ch. (G.)* "affine" of de Man (1887, p. 80, pl. v. fig. 2) from Mergui. Miss Rathbun (1906, p. 872) has suggested that de Man's specimen may belong to *Ch. (G.) japonica* A. M.-Edw.

TEXT-FIG. 15.



Pilumnus sinensis, sp. n., right cheliped of holotype, $\times 4.5$.

PILUMNUS SINENSIS, sp. n.

Material.—1 ovigerous ♀, 24×18.7 mm. (holotype), and 1 ♂, 30×23.4 mm., from Hongkong.

Description.—(a) *Female*. Regions of carapace scarcely indicated ; anterior half covered with long, rather stiff, yellowish-brown bristles. Antero-lateral margin armed with three spines directed forward and outward from expanded bases (text-fig. 14 *a*) ; two spines at outer angle of orbit ; one small spine and two granules on subhepatic region. Front about one-third the greatest width of carapace, divided into two broad inner lobes, separated medially by a V-shaped fissure, and two small triangular outer lobes each terminating in a small spine. Antenna standing in the notch between front and spine of inner orbital angle, being prevented from entering orbital hiatus by a slight upgrowth of the basal segment (text-fig. 14 *a*). Lower orbital border armed with spines on inner half and serrations on outer half ; a group of two spines and some five spinules

beneath the inner three spines. A deep fissure below the two outer orbital spines and two indistinct notches on the upper orbital margin. Right chela (text-fig. 15) considerably smaller than left; 6-7 rows of spines on palm, the larger spines usually curved towards the apex, the smaller conical; three* rows of spines on the proximal upper border of dactylus. The outer surface of carpus of cheliped with numerous curved spines and, projecting far beyond these, bristles similar to those on the dorsal surface of the carapace. Most of these and all the bristles on the upper two-thirds of the palm have been omitted in text-fig. 15. One spine near the distal end of upper margin of the merus. Entire surface of palm of left chela also armed with spines and spinules, with the exception of a small area near the proximal lower border.

TEXT-FIG. 16.



Pilumnus sinensis, sp. n., apex of (a) anterior and (b) posterior ♂ abdominal appendage
c, *Pilumnus spinohirsutus* Rathbun, apex of anterior ♂ appendage, $\times 45$.

Walking-legs thickly covered with bristles similar to, but somewhat more slender than, those on the carapace; no spines on the merus-joints.

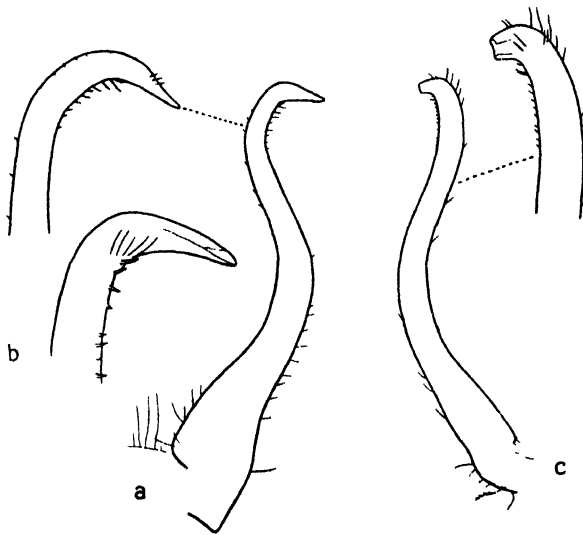
(b) *Male*. Bristles stiffer and darker in colour; of the two spines at the outer orbital angle the dorsal is the more prominent. Chelipeds more nearly equal in size, the left somewhat smaller than the right; eight to ten rows of spines on the palm; proximal half of fingers more spinose on the left than on the right chela. Abdomen long and slender, the terminal segment nearly equal in length to the sum of the two preceding ones (text-fig. 14 b). The anterior

* The third row is poorly developed in the smaller chela and is not visible in the text-figure.

pair of abdominal appendages long and slender, distal half perfectly straight. The apex of one of these is represented in text-fig. 16 *a*. The second pair (text-fig. 16 *b*) is relatively short, about one-fourth the length of the preceding pair.

Remarks.—These specimens do not appear to belong to any of the numerous species of *Pilumnus* already known. They are nearly related to *P. orbitospinis* Rathbun (1911, p. 229, figs. 14 & 15, pl. xvi), which is known only from the ♀. But, from the photographs given, the latter species does not appear to have nearly such long curved spines on the palm and wrist of each cheliped. Moreover, Parisi (1916, p. 185) states that there are one to three

TEXT-FIG. 17.



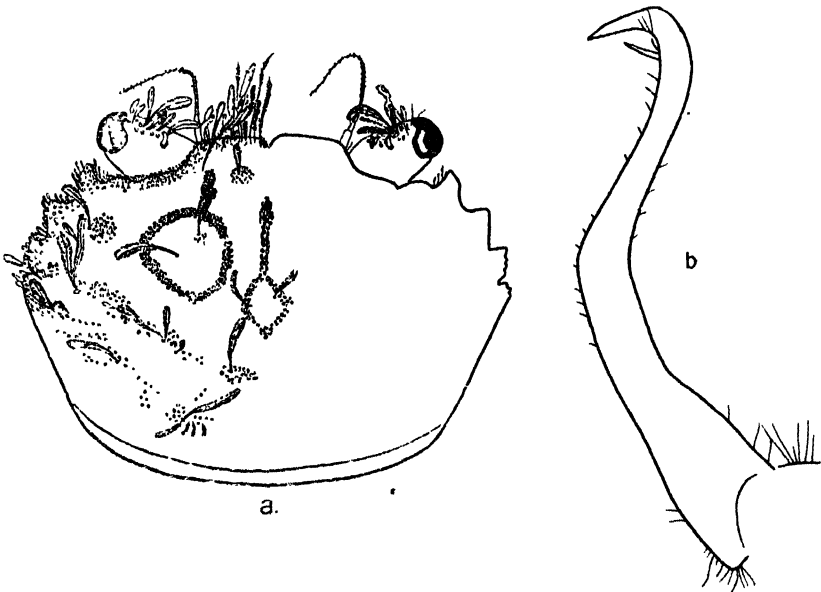
Anterior ♂ abdominal appendage of: *a*, *Pilumnus seminudus* Miers from Hongkong; *b*, apex of same in a much larger type-specimen in 'Alert' collection; *c*, *P. quadridentatus* de Man, co-type. ($\times 27$ and 45 .)

spines on the merus of the walking-legs. *P. orbitospinis* is characterised by the presence of two spines near the distal extremity of the upper margin of the arm. In *P. sinensis*, in addition to the spine already mentioned, there is a smaller spine, and sometimes, in addition, two spinules at the point of articulation with the wrist; the series of small teeth that precedes the spines in *P. orbitospinis* (Parisi, 1916, p. 185) are absent in the Chinese specimens.

Of the species represented in the British Museum Collection, that which most resembles the present species is *P. spinohirsutus* Rathbun from San Francisco. In the latter species there are, however, (1) three spines on each median frontal

lobe; (2) two spines on the upper orbital margin in addition to those at the inner and outer angles; (3) some six spines on the lower orbital border; (4) one or two rows of spines on the carpus and a few smaller spines on the propodus of each walking-leg. In addition, all the spines are horny and dark brown in colour, whereas in *P. sinensis* they are of the same colour as the carapace and slightly calcareous. The ♂ abdomen is also different, the seventh segment being only as long as broad and the anterior abdominal appendage curved outward and downward at the apex (text-fig. 16 c); one of the spines posterior to the apex is very long.

TEXT-FIG. 18.



Pilumnus penicillatus, sp. n.

a, dorsal aspect of carapace of holotype, $\times 15$; b, anterior ♂ abdominal appendage, $\times 45$.

PILUMNUS SEMINUDUS Miers.

Miers, 1884, p. 222, pl. xxi. fig. C; 1886, p. 161.

This species is represented by a number of small individuals, the largest of which is only 7 mm. in breadth, from Hongkong. As stated by de Man, this species differs from *P. quadridentatus* (de Man, 1895, pp. 537-544) chiefly in having three instead of four teeth on the antero-lateral border. On comparing small specimens of *P. seminudus* with co-types of de Man's species from Pontianak, Borneo*, the carapace in the latter proves to be somewhat

* Obtained from Lübeck Museum.

broader in proportion to the length, and narrows considerably more posteriorly. Apparently the ♂ abdominal appendages also differ somewhat (*cf.* text-fig. 17 *a* & *c*). The males were of approximately equal size, but the appendage is less fully developed in *P. quadridentatus*.

PILUMNUS PENICILLATUS, sp. n.

Material.—Holotype (♀, text-fig. 18 *a*) ; 1 ovigerous ♀, measuring approximately 5 mm. in breadth and 1 ♂.

Description.—A small, unusually hairy species with numerous long feathered or brush-like setæ on all thoracic appendages (maxillipeds excepted) ; similar setæ on eye-stalks, front, and scattered over the dorsal surface of carapace. Body and limbs everywhere covered with a fine pubescence ; in addition, a characteristic arrangement of rather long club-shaped outgrowths on dorsal surface of carapace (diagrammatically represented in text-fig. 18 *a*). This pattern, of which the most striking features are the longitudinal median strand ending in a diamond, and the circle or ocellus on either side of this, is very similar in both sexes. Teeth of antero-lateral border concealed by the pubescence ; when carapace is cleaned they are seen to be four in number (see text-fig. 18 *a*). Two distinct notches in the upper, one in lower, border of orbit. Arcolation of carapace very faintly indicated. Antennal flagellum with sparse delicate setæ. Chelipeds nearly equal in both sexes, an unusual occurrence in small species of this genus. A number of longitudinal rows of small white granules on outer surface of palm ; of these four or five along the upper margin are most conspicuous, and can be seen without removing the hairy covering. Small granules here and there on upper outer surface of wrist, which bears no spine. All seven segments of ♂ abdomen separate, the anterior appendage well developed and chitinised, although the specimen is under 5 mm. in breadth (text-fig. 18 *b*) ; the genital duct appears to open at the base of the last thoracic limb. Colour light brown.

Locality.—Hongkong.

Medæus granulosus (Haswell), *Xantho exaratus* (M.-Edw.),
and *Xantho distinguendus* de Haan compared.

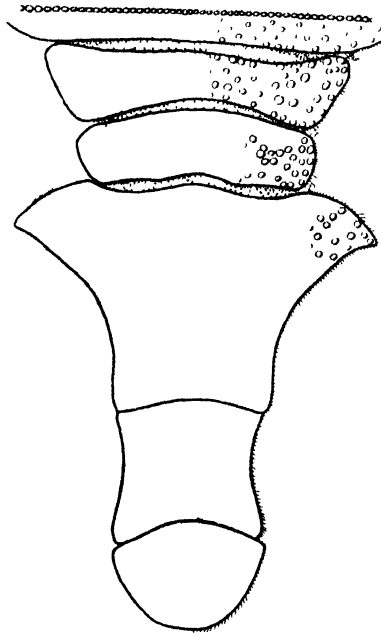
Odhner (1925, p. 81) has concluded that specimens referred erroneously by various authors to *Xantho distinguendus* de Haan belong to the genus *Medæus* Dana. The species in question, *Medæus granulosus* (= *Leptodius granulosus* Haswell, 1882) has four synonyms (see Odhner, 1925, p. 81) ; of these "*Xantho macgillivrayi*" Miers (1884, p. 211, pl. xx, c) and "*Lophozozymus bellus* var. *leucomanus* Lockington" (Miers, 1886, p. 115, pl. xi, fig. 1, and Lanchester, 1900, p. 736) are represented by specimens in the British Museum Collection. There are in the Barney Collection, in addition to specimens of *Medæus granulosus* (Hasw.), specimens that appear to be identical with *Xantho distinguendus* de Haan. Since these two species show a superficial resemblance to each other

and also to *Xantho exaratus* (= *Leptodius exaratus* A. M.-Edw.), a comparison of all these three is given below :—

<i>Medarus granulatus.</i>	<i>Xantho exaratus.</i>	<i>Xantho distinguendus.</i>
1. Fingers sharp-pointed.	Fingers spoon-shaped.	Fingers spoon-shaped.
2. Pterygostomium with short sparse hairs; a few short simple hairs on meri of thoracic appendages.	Pterygostomium, upper and lower margin of arm, and upper margin of meri of walking-legs heavily fringed with setose hairs.	Adult specimens as in <i>X. exaratus</i> .
3. Numerous short transverse rows of bead-like granules on anterior half of carapace; more scattered granules on lateral part of branchial region; beading conspicuous on posterior border, between antero-lateral teeth, and extending on to subhepatic region.	Granules uniformly distributed over carapace becoming smaller posteriorly and in centre—not arranged in rows.	Granules small, uniformly distributed on anterior part of carapace, occasionally forming short transverse rows; faint granulation on lateral branchial and on subhepatic regions.
4. Antero-lateral lobes more prominent and acute than in either of the other two species.		
5. Raised rows and patches of beaded granules on dorsal surface of palm, carpus, and part of merus of chelipeds.	Granular areolation of chelipeds simpler and much less pronounced.	Granulation of chelipeds almost obsolete.
6. Upper margin of merus of walking-legs crested.	Upper margin of merus of walking-legs not crested.	Upper margin of merus of walking-legs not crested.
7. Longitudinal raised ridges of granules separated by distinct depressions, on carpus and propodus of walking-legs.	Raised patches of granules fewer, less regular, and less distinct.	Hardly any trace of the granulation.
8. Abdomen of ♂ as represented in text-fig. 19.	Abdomen of ♂ as represented in text-fig. 20.	Abdomen of ♂ as represented in text-fig. 21.
9. First ♂ abdominal appendages as represented in text-fig. 22 A.	First ♂ abdominal appendages as represented in text-fig. 22 B.	First ♂ abdominal appendages as represented in text-fig. 22 C.

The abdomen of the ♂ *Xantho distinguendus* closely resembles that of *Medæus granulosus*, but they may be distinguished from each other by the difference in shape of segments 6 and 7. In *Xantho exaratus* the abdomen is relatively narrower; segments 3-6 are more elongated than in either of the other two species; heading is almost absent on the proximal segments and segment 2 has a characteristic form (text-fig. 20, cf. text-figs. 19 & 21). Males of the three species can readily be distinguished from each other by the first abdominal appendages (text-fig. 22 A-C); even very small specimens 6-10 mm. broad exhibit the same types of appendages as do adults. In all three species the second abdominal appendage is of the type represented in text-fig. 22 C, 2, and is only one-fifth to one-third the length of the anterior one.

TEXT-FIG. 19.

*Medæus granulosus* (Haswell), ♂ abdomen, $\times 6$.

CATOMETOPA.

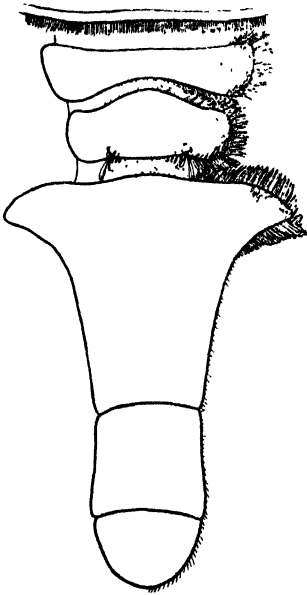
LITOCHEIRA AMOYENSIS, sp. n.

Material.—1 ♂ measuring 6.4×4.6 mm.

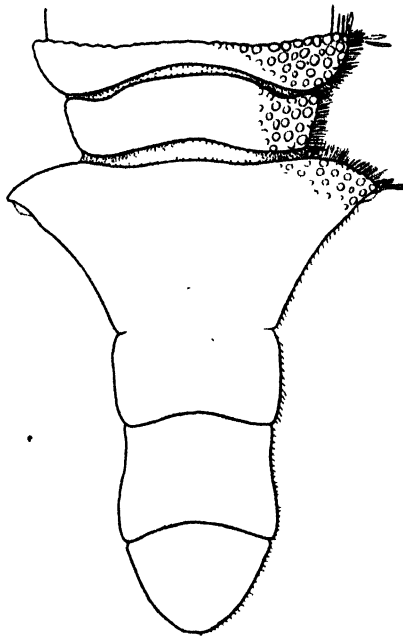
Description.—Carapace quadrilateral (text-fig. 23), covered anteriorly and laterally by a very short, light brown felt which also fills in the shallow grooves, rendering the areolation distinct: fronto-orbital width slightly less than the length of the carapace; antero-lateral considerably shorter than postero-lateral border; outer orbital angle slightly pronounced, rounded and confluent with

the long anterior lobe of the antero-lateral border ; the second lobe is succeeded by two teeth, of which the anterior is well developed. When the short felt is removed, the upper orbital border is slightly undulating in the outer half, perhaps indicating the presence of one or two closed, obsolete notches ; lower border entire (text-fig. 24). Eye-stalk broadened at base (text-fig. 24), freely movable in orbit. Chelipeds approximately equal ; palm and base of each finger somewhat more heavily felted than dorsal surface of carapace, faintly granulose beneath ; fingers white where free from down, two sulci on fixed one. The long silky hairs characteristic of the genus occur

TEXT-FIG. 20.



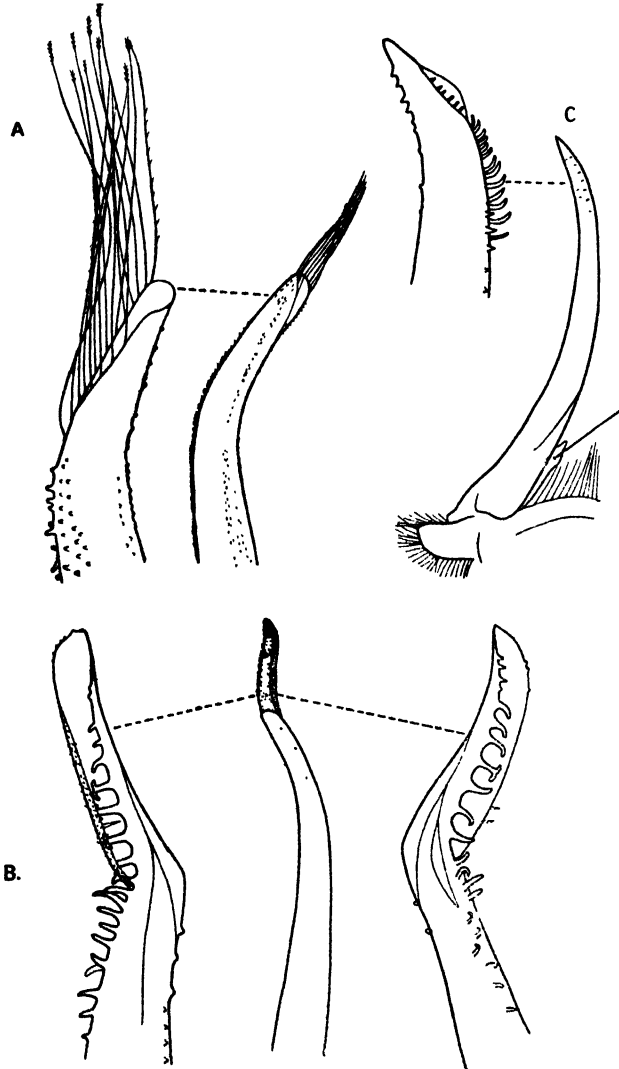
TEXT-FIG. 21.

Fig. 20.—*Xantho exaratus* (A. M.-Edw.) ; ♂ abdomen, $\times 6$.Fig. 21.—*Xantho distinguendus* de Haan. ♂ abdomen, $\times 12$.

on palm, wrist, and walking-legs ; on the carapace they appear to be restricted to a single row parallel to the front, but most of these have been rubbed off ; there are much shorter setæ along the antero-lateral border. The first abdominal segment covers all the space between the fourth pair of walking-limbs ; the anterior abdominal appendages cross over near the apex which is turned inwards (text-fig. 25 c *) ; the genital duct passes forward from the base of the last leg along a wide shallow groove in the sternum.

* See p. 526.

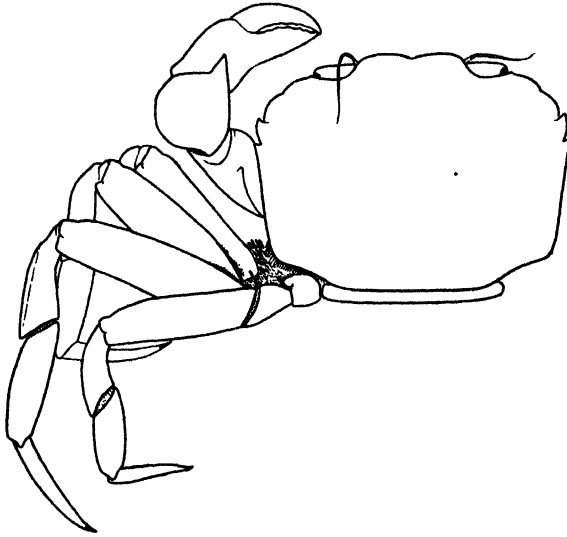
TEXT-FIG. 22.



Anterior ♂ abdominal appendage of: A, *Medæus granulatus* (Haswell); B, *Xantho exaratus* (A. M.-Edw.); C, *Xantho distinguendus* de Haan; 2, second appendage seen behind first. ($\times 15$ and $\times 45$.)

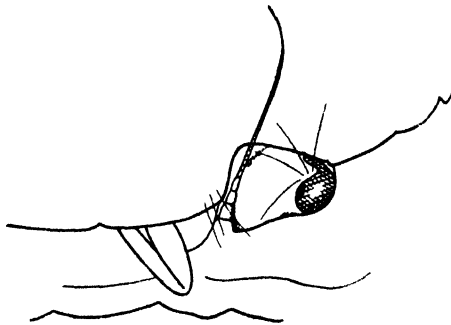
Remarks.—This specimen does not appear to agree with any of the species mentioned in Tesch's key (1918 *a*, pp. 163–5); although most nearly related to the *L. ciliata*, *angustifrons*, *cristata* group (p. 163) it differs from all three

TEXT-FIG. 23.

*Litocheira amoyensis*, sp. n., $\times 6$.

in having the third division of the antero-lateral border prominent and acute, not truncated. It differs from *L. subintegra* Lanchester in (1) being less hirsute; (2) having longer dactyli and narrower propodi on the last pair of walking

TEXT-FIG. 24.

*Litocheira amoyensis*, sp. n., portion of carapace viewed from in front, $\times 15$.

appendages (in *L. subintegra* the propodus is two-thirds as broad as long and the dactylus is three-fourths the length of the propodus—*cf.* text-fig. 23); (3) having the third tooth of the antero-lateral border more prominent and

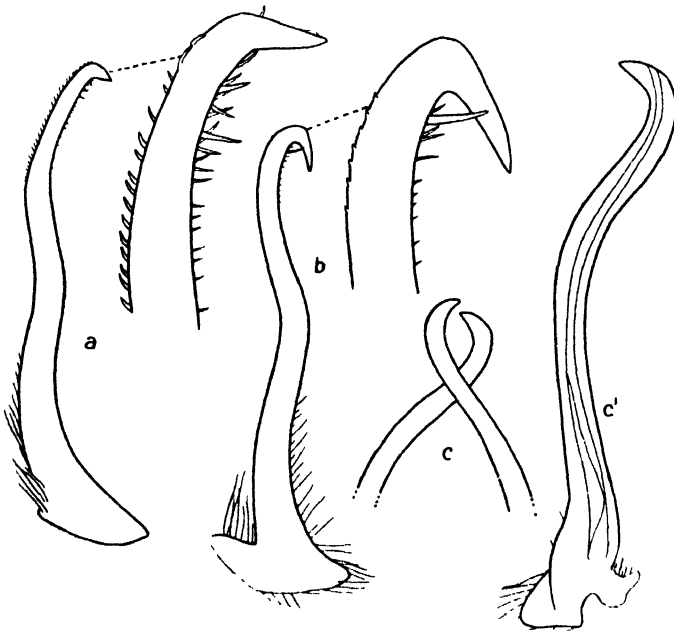
acute; (4) having a rather longer fronto-orbital border and the front less deflexed. Moreover, the anterior abdominal appendages cross over near the apex (text fig. 25 c), whereas in *L. subintegra* * (Lanchester, 1900, p. 750) and *L. subintegra* var. *hirsutior* (Lanchester, 1900, p. 751) these appendages are in contact along the distal third of their length and the apex of each is bent outwards (text-fig. 25 a & b).

MACROPHthalmus TESCHI Kemp.

Kemp, 1919, p. 393, pl. xxiv, figs. 8 & 9.

A single ♂, measuring 27 × 18 mm. was referred by Barney to *M. teschi* Kemp. It differs from that species in the following respects :—(1) the upper

TEXT-FIG. 25.



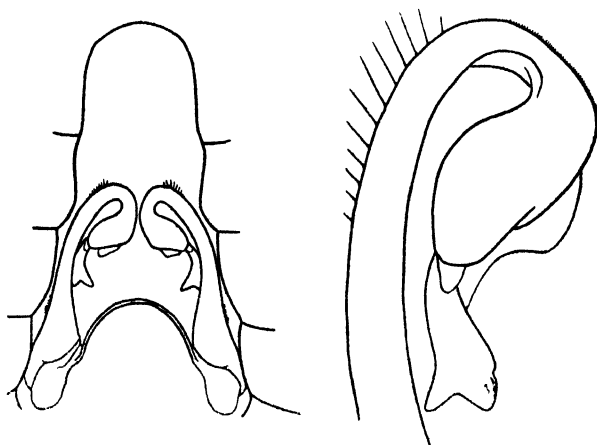
Anterior ♂ abdominal appendage of: *a*, *Litocheira subintegra* var. *hirsutior* Lanchester; *b*, *Litocheira subintegra* Lanchester; *c*, *Litocheira amoyensis*, sp. n.; *c*, apex of anterior pair of ♂ appendages of *L. amoyensis* in natural position as they rest on the sternum. (*a* & *b*, × 15 and 45; *c*, × 35.)

orbital border is not so straight as is shown in Kemp's figure; (2) the inner row of granules on the branchial region is broken in the centre; (3) the first three pairs of walking-legs are more heavily furred, so that the minute spinule near the distal end of the upper margin of the merus is concealed, while a minute

* This species is not the same as *L. integra* (Miers). for Miers's type-specimen (1884, p. 543, pl. xlviii, C) shows no trace of teeth on the antero-lateral border, while the width of the fronto-orbital border is considerably more than the length of the carapace.

spine is also present on the merus of the last limb ; (4) the antero-lateral border is more conspicuously crenulated ; (5) there are several rows of minute crowded granules, each with the apex of a darker colour than the base, along the dorsal margin of the palm and dactylus of the chela ; similar, more prominent granules

TEXT-FIG. 26.



TEXT-FIG. 27.

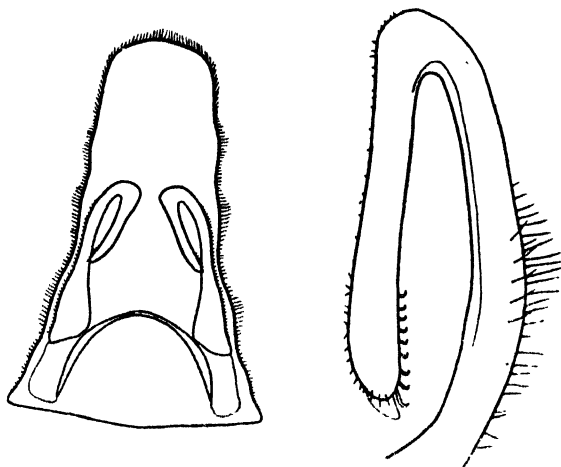


Fig. 26.—*Paracleistostoma depressum* de Man, anterior ♂ abdominal appendages ($\times 6.5$) and apex of one of these ($\times 27$).

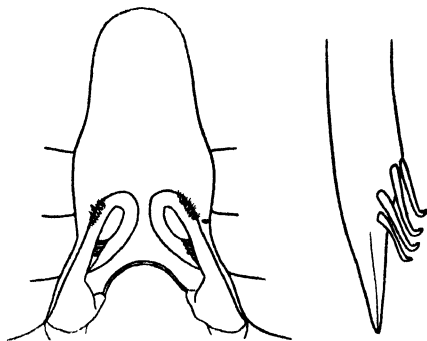
Fig. 27.—*Paracleistostoma leachi* (Audouin), anterior ♂ abdominal appendages resting on abdomen ($\times 6.5$) and enlarged view of apex of one of these ($\times 27$).

are present on the lower border of the palm and are continued on to the proximal inner surface as well as on to the proximal half of the immovable finger.

The carapace is 1.5 times as broad as long ; in *M. teschi* from 1.52–1.64 times (see Kemp's measurements, 1919, p. 394).

These differences are slight and, until more material from the Indian and Pacific Oceans is available, it seems best to refer this Chinese specimen to *M. teschi*. It also shows affinities with *M. japonicus* de Haan, but cannot

TEXT-FIG. 28.

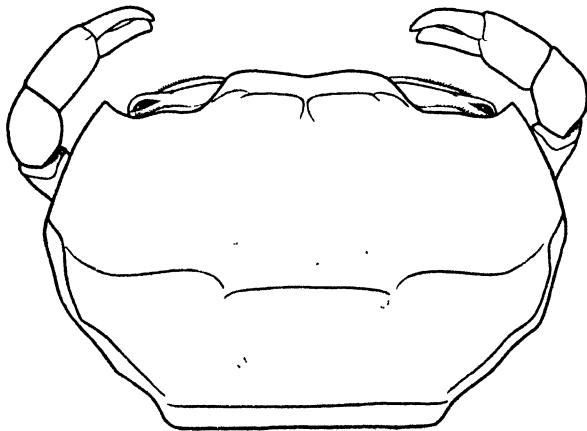


Paracleistostoma cristatum (Ortmann) de Man, anterior ♂ abdominal appendages of a type-specimen ($\times 6.5$) with enlarged view of apex of one of these ($\times 27$).

be identified with that species because the inner surface of the palm and fingers is heavily felted.

Previously recorded from Port Canning, Arakan Coast, and Mergui.

TEXT-FIG. 29.



Paracleistostoma cristatum (Ortmann) de Man, carapace in dorsal aspect and chelipeds of a type-specimen, $\times 6$.

PARACLEISTOSTOMA DEPRESSUM de Man.

de Man (1895) pp. 581-590, pl. xiv, fig. 13 in Bd. 9, 1896; Tesch (1918) p. 63, in key.

In the Peking collection are two ♂♂ which have been compared with co-types from Pontianak, Borneo, received in exchange from Lübeck Museum. In the

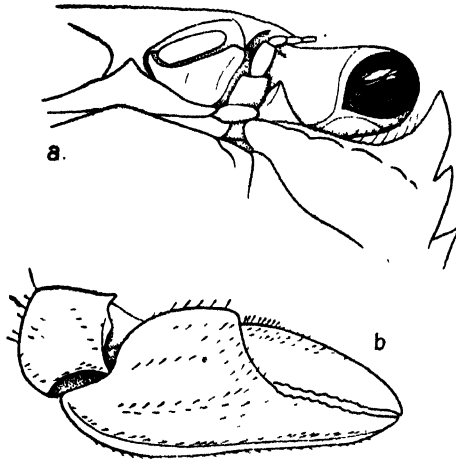
three species of this genus of which specimens have been examined the anterior ♂ abdominal appendages* are so strikingly different that figures of these are given. Text-fig. 26 represents these appendages in *P. depressum* de Man; text-fig. 27 in *P. leachi* (Audouin), and text-fig. 28 in *P. cristatum* de Man (1895, pp. 590–595=*Cleistostoma dilatatum* Ortmann, nec de Haan). Since the latter species has never been figured, the carapace of a co-type, in dorsal aspect, is represented in text-fig. 29 by permission of the authorities of the Strasbourg Museum.

BRACHYNOTUS PENICILLATUS de Haan.

For references see Tesch (1918) p. 104; Yokoya (1928) pp. 780–781, text-fig. 8.

Two ♂♂ from Amoy, two ♂♂ and one ♀ from Hongkong, agree with *B. brevidigitatus* Yokoya in having the dactylus shorter than twice the dorsal

TEXT-FIG. 30.



Brachynotus longitarsis Miers.

a, part of anterior ventral surface of carapace to show infraorbital ridge;

b, chela. $\times 15$.

length of the palm, the front sinuous and the morus of the outer maxilliped partially concealing the exognath. The infraorbital crest is the same as in *B. penicillatus* (Tesch, 1918, p. 104, key), and the differences are so slight that Yokoya's species should, in all probability, be included in *B. penicillatus* de Haan.

Since Tesch (1918, pp. 104–5) was unable to include *B. longitarsis* Miers (1879, p. 37, pl. ii, fig. 3) in his key because the infraorbital ridge had not been described, a note on Miers's species may conveniently be added here, although it is not represented in the Chinese collections. In the ♂ the infraorbital ridge is divided into six or seven lobes; the first is faintly crenulate and only indistinctly marked off from the short second lobe (text-fig. 30 a); the third

* See p. 525.

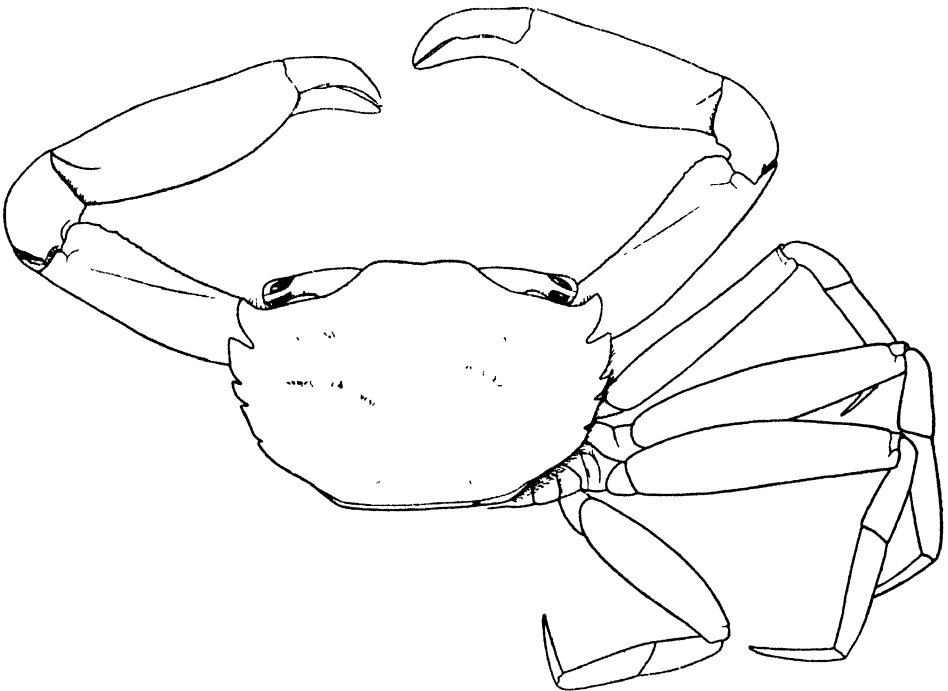
and fourth are about equal in length and longer than the second; the succeeding ones rapidly diminish in size, so that the seventh, when present, is extremely minute. Thus *B. longitarsis* is allied to the *B. harpax*, *penicillatus*, *oregonensis* group (Tesch, 1918, p. 104), but has the infraorbital ridge divided into six or seven instead of three or four lobes.

In the ♀ the ridge is regularly serrate and divided into some eighteen short lobes.

METAPLAX SHENI, sp. n.

Material.—2 ♂♂, measuring 13.2 × 8.6 mm. (holotype) and 12.8 × 8.5 mm. respectively.

TEXT-FIG. 31.



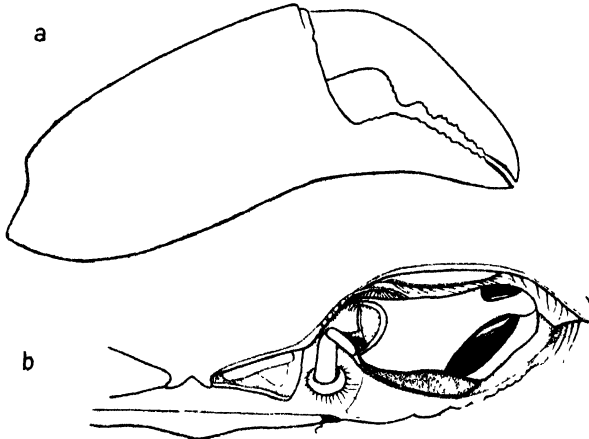
Metaplex sheni, sp. n., holotype in dorsal aspect.

Description.—Tesch (1918, pp. 116–117), who has revised the genus *Metaplex* H. M.-Edw., found that the infraorbital margin in the ♂ was “of great systematic value.” The ♂♂ from China cannot be identified with any of the species in Tesch’s key. The infraorbital crest (text-fig. 32 *b*) is divided into fifteen to nineteen lobules; the first of these, by far the largest, is faintly crenulate on the inner half; the second is about half the length of the first; the third to fifth gradually decrease in size and thereafter they are small and bead-like.

Text-figs. 31 and 32 give a good idea of the general appearance of the holotype, so that no lengthy description is required. The position of the species in Tesch's key may be mentioned: it would come into his second division thus:—

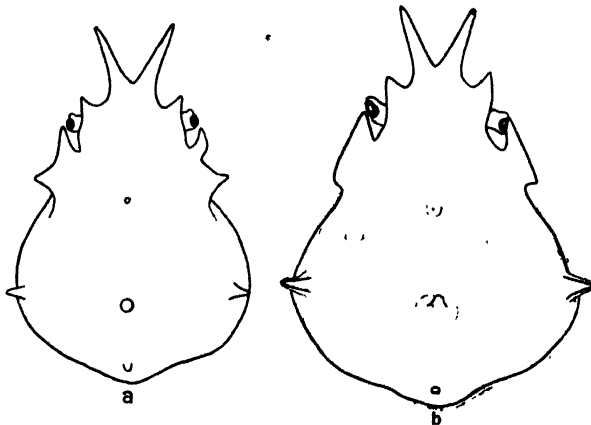
2. No. of lobules of the infraorbital ridge of ♂ 7–9 3.
 No. of lobules of the infraorbital ridge of ♂ 15–19 *M. sheni*.
 No. of lobules of the infraorbital ridge of ♂ exceeding 20 4.

TEXT-FIG. 32.



Metaplar sheni, sp. n., holotype. a, smaller chela, $\times 10.5$; b, portion of anterior border of carapace to show infraorbital ridge, $\times 8.5$.

TEXT-FIG. 33.



a, *Pugettia minor* Ortmann, ♀ (length 11 mm.), dorsal aspect of carapace;
 b, *Pugettia cristata*, sp. n. $\times 4$.

It is thus most nearly allied to *M. dentipes* (Heller) and *M. distincta* H. M.-Edw., both of which have twenty-five to thirty lobules, but differently arranged.

Locality.—Amoy.

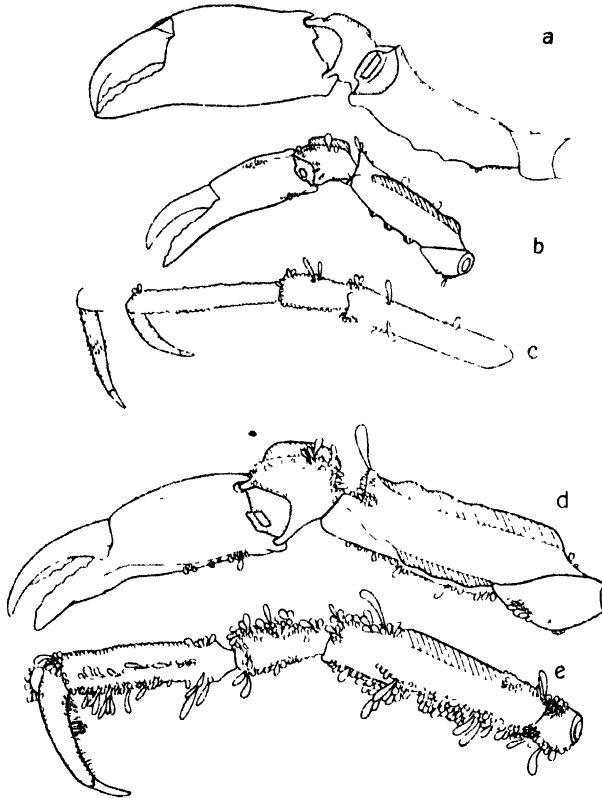
OXYRHYNCHIA.

PUGETTIA CRISTATA, sp. n.

Material.—2 ovigerous ♀♀, measuring 13.0 / 9.6 mm. (holotype) and 13.2 × 9.5 mm.

Description.—Carapace in general outline resembling *Pugettia incisa* de Haan (1833–1850, pl. xxiv, fig. 3), with postorbital process continued backward for some distance as a wing-like outgrowth (text-fig. 33 *b*). Cheliped as represented in text-fig. 34 *d*, with conspicuous crest on the carpus and two crests

TEXT-FIG. 34.



Pugettia minor Ortmann : *a*, cheliped of ♂, *b* of ♀ ; *c*, first walking-leg of ♀. *Pugettia cristata*, sp. n. : *d*, cheliped of ♀ ; *e*, first walking-leg of ♀. (*d*, × 8; others, × 6.)

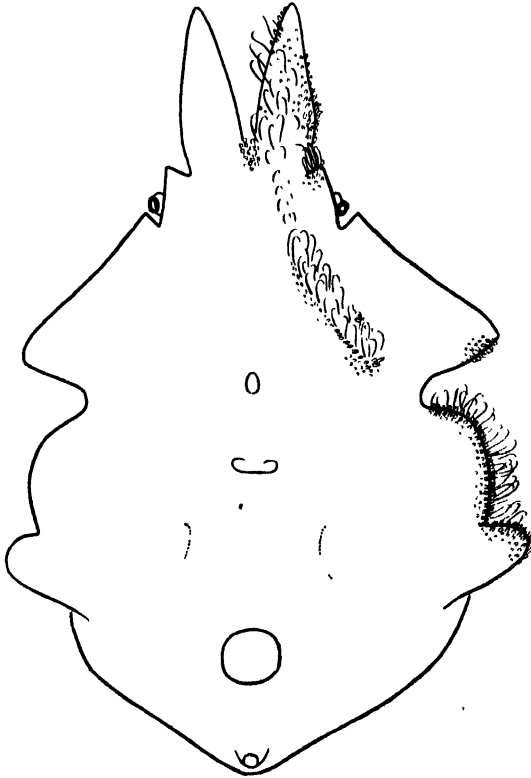
on the merus ; upper and lower borders of palm sharp, approaching to crests. The species is characterised by a high thin crest on the dorsal margin of the merus of the first walking-leg (text-fig. 34 *e*) ; there is a similar, though shorter, crest on the next appendage and on the third limb it is still more reduced or absent, while on the last appendage it is wanting.

Remarks.—These specimens appear to be related to *P. incisa* from Japan, but, from de Haan's figure (1833, pl. xxiv, fig. 3) it would appear that there

are no crests on the meri of the anterior walking-legs. Crests are absent from these appendages in specimens referred to *P. incisa* by Miers (1879, p. 23), as also in a specimen referred to the same species by Ortmann * (1893, p. 44).

It was thought that these small specimens might belong to *P. minor* Ortmann (1893, p. 44), but, on comparing them with two co-types *, this proved not to be the case. Since *P. minor* has not been figured, permission to include illustrations of the carapace (text-fig. 33 *a*) and certain appendages (text-fig. 34 *a-c*) was obtained. In *P. minor* there is a distinct spinous process behind

TEXT-FIG. 35.



Pugettia sagamiensis (= *P. brevirostris* Parisi, nec Doflein).
carapace in dorsal aspect, $\times 3$.

that which forms the posterior boundary of the orbit. The cheliped of the ♀ is rather similar to that of *P. cristata*, but the second crest on the merus is represented by three separate portions (*cf.* text-fig. 34 *b* & *d*). The first walking-leg has no trace of a crest on the merus (text-fig. 34 *c*); there are, however, only a few long vesicular outgrowths and the propodus is longer in proportion to the length of the dactylus than in *P. cristata*.

* Specimens of both species obtained for examination from Strasbourg Museum.

The specimens cannot be identified with *P. quadridens* de Haan, nor with *P. brevirostris* Doflein (1904, p. 85, pl. xxvii, figs. 13, 14) or "*P. brevirostris*" Parisi (1915, p. 287, pl. vii, fig. 1).

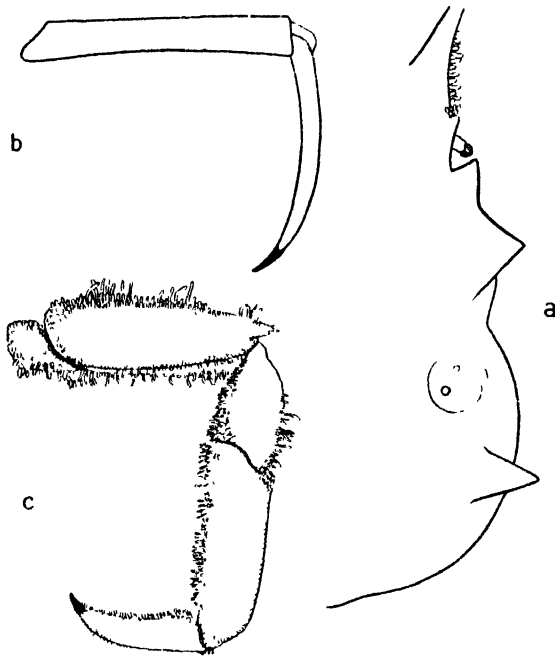
Locality.—Amoy.

PUGETTIA SAGAMIENSIS, nom. nov. (for *P. brevirostris* Parisi, *nee* Doflein).

Parisi, 1915, pp. 287-288, pl. vii, fig. 1, text-fig. 2.

On comparing Parisi's ♂ specimen from Sagami Bay, Japan, with the holotype (♂) of *Pugettia brevirostris* Doflein (1904, p. 85, pl. xxvii, figs. 13 & 14) it is evident that it cannot belong to that species. The carapace of

TEXT-FIG. 36.



Pugettia brevirostris Doflein, type: *a*, right side of carapace; *b*, dactylus and propodus of second walking-leg, denuded; *c*, second walking-leg of *P. sagamiensis*. (*a*, $\times 3$; *b* & *c*, $\times 2.5$.)

P. sagamiensis is closely covered with low, flattened, vesicular outgrowths, which become somewhat more elongated only on certain small areas, as indicated schematically in text-fig. 35, and in no wise mask the general contour of the carapace. In *P. brevirostris*, on the other hand, the vesicular outgrowths are everywhere rather prominent and conceal the lateral outline of the carapace, so that it seems to approach that of *P. sagamiensis*. Doflein had removed these vesicles from the right side so as to expose one-half of the carapace (text-fig. 36 *c*). *P. sagamiensis* differs from *P. brevirostris* in the following respects:—(1) there is a broad wing-like outgrowth posterior to the orbit instead of two

spines (*cf.* text-figs. 35 & 36 *a*) ; (2) behind this the lateral border is drawn out into two lobes, of which the posterior is the shorter and more prominent, whereas in *P. brevirostris* there is a raised mound on the anterior branchial region some distance from the actual border and behind this a distinct branchial spine ; (3) there is but one pronounced eminence on the gastric region followed by a very low elongated ridge (text-fig. 35), whereas in *P. brevirostris* there are five—three median, of which the second is most conspicuous, and a very small one on either side between the first pair of median ones ; (4) the most marked difference, however, is in the shape of the two terminal joints of the walking-legs. In *P. sagamiensis* these joints are much compressed and, again, the flattened scale-like vesicles do not conceal their general form (text-fig. 36 *c*). The upper third to half of the propodus appears to be a crest (shaded in text-fig. 36 *c*), but the lower portion is almost as thin. In *P. brevirostris* the prominent vesicles must be removed before the shape of the joints is apparent ; when denuded both are slender and approximately circular in cross-section.

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Entomological Expedition to Abyssinia, 1926-7 : Coleoptera, Staphylinidæ.
 Systematic Report by Dr. MAX BERNHAUER (Horn, N.-Oe., Austria) ;
 Introduction by HUGH SCOTT, M.A., Sc.D., F.L.S., F.E.S.

[Read 19th March, 1931.]

PART I.—INTRODUCTION. By HUGH SCOTT.

The Staphylinidæ under review were collected by myself and Mr. J. Omer-Cooper, M.A., F.L.S., during our expedition to Abyssinia from August 1926 to February 1927. 123 species, representing 43 genera, are enumerated, and many others have been left undetermined owing to inadequacy of the material. 56 species (representing 23 genera) are described as new, and one new genus is erected, while 56 out of the 67 previously known species are here for the first time recorded from Abyssinia.

In a work entitled 'Zur Staphyliniden-Fauna des Tropischen Afrika' * Dr. Bernhauer described 42 species from Abyssinia, only 7 of which were rediscovered by our Expedition. Thus, in that article and the present report together, 158 species are described or recorded from Abyssinia, while many other descriptions and records have appeared in scattered papers by Dr. Bernhauer and other writers. The number of species of Staphylinidæ occurring in a country so vast, so diversified in topography, altitude, climate and vegetation, may easily run into thousands. It can be recalled in passing that nearly 900 species of this enormous family inhabit the British Islands, while a conservative estimate of the European Staphylinidæ is between 2,600 and 2,800 species.† Without, therefore, attempting to estimate the total Staphylinid fauna of Abyssinia, it appears that only a small part has as yet been brought to light. Our collecting did not touch the lower country, but was confined to altitudes of more than 5,000 feet above sea-level. Many of the localities lay between 7,000 and 10,000 feet, while a few were between 10,000 and 13,000 feet.

Zoogeographical. The Abyssinian fauna, as a whole, though mainly African, includes some Palaearctic and Oriental elements—witness such Northern forms as the Abyssinian ibex (*Capra walie*), only known from the high mountains of Simen, and the chough (*Pyrhocorax pyrrhocorax*), also occurring in some of the highest mountains, but not found (outside Abyssinia) nearer than North-West Africa and Syria : also the Abyssinian loach (*Nemachilus abyssinicus*)

* Ann. Mus. Nat. Hungar. xiii, pp. 95-189 (1915). This work also includes descriptions of 6 species from Eritrea.

† I am indebted for these figures to Commander J. J. Walker, R.N., M.A., F.L.S., who based his estimates on the most up-to-date catalogues available, with due consideration of recent additions.

inhabiting the waters of Lake Tana, sole African representative of a European-Asiatic family of fishes; lastly, the Oriental butterfly *Argynnis hyperbius* [*A. niphe*], found in no other part of Africa but Abyssinia, though it is distributed right across the Orient, from India and Ceylon to Japan, the East Indies, and New Guinea (with a detached area halfway down the Eastern side of Australia). Are these cases solitary relicts and exceptions, or will the small invertebrate fauna prove, when worked out, to contain a mingling of Ethiopian, Palæarctic, and Oriental forms?

So far as Staphylinidæ are concerned, they are highly mobile insects, which readily take wing, and include many very widely distributed species. The family is, therefore, less easy to analyse faunistically than some other groups of Coleoptera, which, having feebler powers of dispersal and including flightless forms restricted to particular habitats, contain a high proportion of species of limited geographical range. Nevertheless, some analysis of our Abyssinian Staphylinid collection from a faunistic standpoint is attempted here.

As to the *genera*, excepting a very few smaller ones (e.g., *Perierpon*, *Tomoxelia*, *Ænictonia*) known only from Africa, or Africa and Madagascar, and the one new genus, all the genera represented are widely distributed, occurring in more than one of the great zoogeographical regions, and in many cases world-wide. Even the new genus (*Hypselusa*) seems to be closely related to genera of wide distribution.

Turning to the *species*, the 56 new ones may be considered first. Dr. Bernhauer alludes to resemblances or differences between many of them and species previously known. About 12 of the new species are said to resemble previously described African—mainly East African—forms, while 13 of the new species (7 of which belong to the great genus *Atheta*) resemble Palæarctic species. There is, however, some doubt how far these external resemblances imply real faunistic relationships, at least until further knowledge, based on the critical intensive study of obscure genera, is available. Still there is at any rate an indication of African and Northern affinities among certain of the new species.

Of the 67 "old" species listed in this paper, I have been able to tabulate the recorded distribution of 64. They fall into three main categories:—

I. VERY WIDESPREAD OR EVEN COSMOPOLITAN.—These, 13 in number,* are of little interest from the present point of view.

II. THE NORTHERN ELEMENT.—9 species, of which 2 † range almost throughout the Northern Hemisphere, while 7 ‡ are Palæarctic; 5 of these are, however, referred to European or Mediterranean species as varietal forms, and in two

* *Atheta sordida*, *Amischa analis*, *Leptacinus batychnus*, *Leucoparyphus silphoides*, *Medon ochraceus*, *Mimogonus fumator*, *Neobisnius procerulus*, *Oxytelus laqueatus*, *Pæderus fuscipes*, *Philonthus longicornis*, *P. nigrifolius*, *Trogophlæus exiguus*, *T. nigrita*.

† *Tachyporus nitidulus*, *Xantholinus punctulatus*.

‡ *Aleochara bilineata*, *Oligota flavicornis*, *Oxytelus piceus*, *Philonthus maritimus* (?), *Scopæus lævigatus*, *Stenus fossulatus* (?), *Tachynusa umbratica*.

cases with some doubt. The genuine Northern element therefore appears very small.

III. THE AFRICAN ELEMENT.—This is by far the largest, including 42 species, which may be further subdivided as follows : (a) 11 species * previously known from Abyssinia ; (b) 21 species recorded from East or South Africa, more than half † only from East Africa (Kenya and Tanganyika), several only from South Africa ‡, and two § from both East and South ; (c) 6 species || all referred, either doubtfully, or as varieties, to species occurring in the Congo or in West Africa ; (d) 4 species difficult to place in any subdivision—namely, *Oxytelus planus* var. *punctulatus*, recorded from Abyssinia, West and South Africa, *Falagria coarcticollis*, Africa, Madagascar, Mascarene Islands and Seychelles, *Pæderus sabæus*, Africa, Arabia and Madagascar, and *Philonthus fimbriolatus*, apparently only recorded previously from Madagascar. The last three of this subdivision may constitute a genuine small Afro-Madagascan element (compare remarks above, under Distribution of the Genera).

To sum up : the most important elements in our collection are a smaller Northern group, comprising Palæarctic species or forms related thereto, and a much larger African group, in which East African species, or forms related to them, strongly predominate. An Oriental element is not apparent, though the slender Afro-Madagascan element may indicate a connexion with the Oriental fauna.

The Palæarctic element would probably have been more marked, had our expedition extended into Northern Abyssinia—the ancient provinces of Abyssinia proper. The occurrence in the Galla provinces further south—in the districts around Addis Ababa and about Lake Zwai, and Mount Chillálo in the Arussi country just east of Lake Zwai, where the material was actually collected—of species previously recorded from Kenya, Tanganyika or South Africa, tallies with the extension of the known range of certain plants brought about by our investigations, for some of the plants collected have been identified as species previously recorded only from East Africa. Probably many wide-ranging species are distributed over the eastern part of the Continent in high places, but discontinuously, not occurring in intervening low-lying tracts. For instance, the Staphylinid *Atheta zukwala* was found only at 9,000 feet on Mt. Zukwala and at the same altitude on Mt. Chillálo, and may not occur on

* *Conosoma discolor*, *Coproporus abessinus*, *C. pinguis*, *Cryptobium athiopicum*, *C. errerense*, *Nudobius abessinus*, *N. coloriventris*, *Pæderus duplex*, *Stilicus clarissimus*, *Zyras laminatus*, *Z. regalis*.

† *Acylophorus orientalis*, *Ænictonia vosseleri*, *Cardiola csikii*, *Cryptobium nairobiense*, *Omalium algidum*, *Oxytelus fulgidus*, *O. miriceps*, *Pæderus crebrepunctatus*, *P. rufocyanus*, *P. scabripennis*, *Philonthus minutissimus*, *Scopæus peregrinus*, *Stilicus schimperi*.

‡ *Acanthoglossa brevicollis*, *Astemus tropicus*, *Hypocyrtus capensis*, *Oxytelus bidentulus*, *Perierpon hewitti*, *Philonthus bisignatus*.

§ *Aleochara rufipes*, *Stenus rorellus*.

|| *Medon fulvus* (?), *Myllæna africana* (?), *Oxytelus grandis* (?), *Stilicus rubellus*, *Tomoxelia bisulcata*, *Zyras nitidipennis*.

the nearly 50 miles' width of plateau separating these mountains, which is 2,000–3,000 ft. lower, much hotter and drier, and covered largely with thorn-scrub, absolutely different from the forest and heath-land of the mountains.

The wide but discontinuous distribution of some species over the high parts of East Africa does not preclude the existence of other more narrowly localised forms, each confined to its own particular mountains or high plateau. Species of such restricted distribution are less likely to be evolved in a family of very mobile insects, like Staphylinidae, than in other groups with more sluggish habits and less power of dispersal (*e. g.*, certain groups of flightless weevils). It may be remembered, however, that some of the new species appear to be allied to, but distinct from, species occurring in Kenya or Tanganyika.

These findings may be compared with the conclusions arrived at in the study of the Collembola.* 15 species are known from the Abyssinian highlands (12 of them were obtained by our Expedition) and 13 are apparently endemic. Putting aside one cosmopolitan species, they exhibit no affinity with Palaearctic forms, but their relationships are almost entirely with the fauna of the other mountainous parts of Eastern Africa. The investigation of them has established a connexion between the previously nearly isolated Collembolan fauna of the Seychelles and that of the African continent—which is remarkable, since most groups of Seychelles insects present Oriental rather than African affinities.

Again, among the twenty-seven species of aquatic Hemiptera collected, two have clear Palaearctic affinities, while the remainder are Ethiopian. The two former were found, respectively, in streams flowing into a tributary of the Blue Nile and in a pond very little south of the watershed, so possibly these northern insects have worked their way southwards up the Blue Nile to the Abyssinian highlands.†

Ecological.—Under this head not many general results can be drawn from an expedition lasting only a few months. It would be of little use at present to burden this Introduction with lists of species associated with, respectively, dense forests at about 8,000–9,600 feet elevation, treeless heath-land above 10,000 feet, beds of rivers and flood-rubbish, margins of mountain-torrents, and the shores of lakes at 5,000 to 7,000 feet, though lists could be made out for all these types of habitat. Many species were found in the kind of environment that might be expected from a knowledge of the habits of their genera in other parts of the world. Numerous specimens of certain new species (*e. g.*, *Leptacinus micropterus* and *Atheta altissima*) were found on the bare heath-land at the summit of Mt. Chillálo, at an altitude of 12,000 to 13,000 feet, and very few specimens of these forms elsewhere. Examples of *Leptacinus cooperi* and two species of *Zyras* were caught through their flying to artificial light in our tent.

* Handschin, Trans. Ent. Soc. lxxvii, pp. 15–28 (1929).

† G. E. Hutchinson, Proc. Zool. Soc. pp. 437–466 (1930).

Fauna of Tree-Euphorbias and Tree-Lobellias.—Special attention was devoted to the Coleoptera and other animals found in the dead parts of these plants.

(i) TREE-EUPHORBIAS.—Material was collected from the tree-Euphorbias of Abyssinia for comparison with the Euphorbia-fauna of Morocco, and Madeira and the Canaries, to which further reference is made below. All the trees examined belonged to a single species, *Euphorbia abyssinica* Rausch., the great cactus-like *kolkoual*, which reaches a height of 30–40 feet. Those first investigated were growing under purely natural conditions, in a shady and moist situation, among the dense forest-vegetation of giant *Juniperus*, *Podocarpus*, etc., at an altitude of 8,000 feet, in Jem-Jem Forest. Others formed a tall hedge in open, nearly treeless surroundings, but close to houses, at Lake Haramaiya, *circa* 6,600 feet. Among the organisms found in their dead branches were twelve species of Staphylinidæ, viz.:—*Oxytelus fulgidus* Fauv., *Paderus crebripunctatus* Epp., *Medon abessinus*, sp. n., *Leptacinus batychnus* Gyll., *Nudobius abessinus* Fauv., *Conosoma* sp. (one example), *Homalota densicollis*, sp. n., *Fulagria coarcticollis* Fauv., *Atheta* (s. str.) *euphorbiæ*, sp. n., *Atheta* (s. str.) *haramaiyana*, sp. n., *Atheta* (*Coprothassa*) *zukurulana*, sp. n. (small form ?), and one specimen of doubtful generic position. The most interesting are *Atheta euphorbiæ* and *A. haramaiyana*, both of which may prove to belong to a special euphorbiculous fauna. Thirty-four examples of the former were obtained from tree-Euphorbias and only one specimen in a different *milieu*, where it may well have been an accidental wanderer: only two examples of the latter were taken, both of them from tree-Euphorbias. All the other named species were found in other habitats besides Euphorbias, and nearly all are geographically wide-spread. If the search for beetles peculiar to these plants proved somewhat disappointing, so far as Staphylinidæ are concerned, it must be remembered that Staphylinidæ form only a small proportion of the extensive list of euphorbiculous Coleoptera of Morocco and the Atlantic islands. The only exclusively euphorbiculous Staphylinid recorded from Southern Morocco, *Atheta* (*Hilara*) *repentina* Peyerimhoff, belongs to the same genus as those from Abyssinia. The two exclusively euphorbiculous species known from the Atlantic islands belong, respectively, to the genera *Homalota* and *Omalium*.*

To explain why Morocco, Madeira and the Canaries are chosen for comparison, it may be added that the classical work of T. V. Wollaston on the Coleoptera of the arborescent, shrubby and cactiform Euphorbias of the islands has been followed recently by a comparative examination of those of the Euphorbias of Southern Morocco. Collections made in the Sus by Alluaud and others have been discussed by de Peyerimhoff †, whose systematic account is prefaced with some general remarks on this type of "biocœnosis" or "association." The euphorbiculous Coleoptera are grouped in three categories (xylophagous,

* de Peyerimhoff, Bull. Soc. Sci. Nat. Maroc, iii, p. 49 (1923). Eight other species were listed by Wollaston ('Coleoptera Atlantidum,' 1865, pp. xxxiii, xxxiv), but are not exclusively euphorbiculous.

† *Op. cit.*, pp. 43–63 (1923); v, pp. 8–14 (1925) and pp. 153, 154 (with plate) (1926).

predaceous and commensal), and the Staphylinidæ (which are believed to be either enemies of Acarines or saprophagous) fall under the last head. A result of this later work is to show that the beetle-fauna of the Euphorbias of the Atlantic islands exhibits, on the whole, a less degree of endemism than was supposed, though it appears even more interesting than formerly from an ecological standpoint.

(ii) **TREE-LOBELIAS.**—The plant investigated, one of the most remarkable in the Abyssinian flora, is that referred to in some books on travel in Abyssinia as *Rhynchoptalum montanum*, but, more correctly, *Lobelia rhynchoptalum*.* I only met with it once, a solitary clump close to a group of great rock-pillars on the desolate heath-covered summit of Mt. Chillalo, at an altitude of 12,000–13,000 feet. The plants, which were not in flower, had hollow woody stems about 4 feet high and dense crowns of leaves like those of a Yucca.† Coleoptera and the maggots and puparia of a small fly (Drosophilidæ) were found in the wet decaying substance under the loose bark of some dead stems. The beetles comprised a series of a Cryptophagid, *Cryptophagus* (subgenus *Mnionomus*) sp., and four species of Staphylinidæ, viz.: *Megarthus abessinus*, sp. n., *Omalium algidum* Fauv., *Atheta* (s. str.) *lobeliae*, sp. n., and *Atheta* (*Coprothassa*) *paludosa*, sp. n.

Megarthus abessinus and *Omalium algidum* were, doubtless, chance visitors, since in both cases more specimens were found in other habitats than those taken from Lobelia-stems (the *Omalium* was originally recorded from Kilimanjaro, where it may occasionally infest dead stems of other species of the tree-Lobelia). In the case of *Atheta paludosa*, several were found in the Lobelia-stem and several on the surrounding heath-land. All the examples of *Atheta lobeliae*, five in number, were collected from the Lobelia. These two species of *Atheta* may well form part of a special lobelicolous fauna (*Atheta*, it will be recalled, is also one of the few genera of Staphylinidæ represented in the Euphorbia-fauna).

Species found in Ants' Nests.—The few such insects brought to light by our general collecting include two species of Staphylinidæ, each represented by

* *R. montanum* Fresen (1838) = *L. Rhynchoptalum* Hemsley (in Oliver, Flor. Trop. Afr. iii, p. 465, 1877).

† A. B. Wylde writes ('Modern Abyssinia,' chap. xv, pp. 345, 346, 1901) that the native name of the tree-Lobelia is *gvara* and that the hollow stem is used by boys as a trumpet. He gives the height of a large specimen as 8 feet for the bare stem, 6 feet for the crown of leaves, and perhaps 8 feet for the spike of small pale blue flowers, or about 22 feet in all. These plants seem to require an altitude above sea-level of 12,000 feet or more, and I saw none in the mountains of Entoto behind Addis Ababa, or in those above Jem-Jem Forest, where the altitude is only 9,000 to 10,000 feet. These Lobelias figure in old drawings of landscapes in Simen in works on travel in Abyssinia, such as pl. vi of 'Abbildungen zur Reise in Abyssinien von Dr. E. Rüppell' (1840) and 'Views in Central Abyssinia . . . with Descriptions by Sophie F. F. Veitch' (1868). H. C. Maydon found them in straggling groups on the edges of the vast precipices which bound the table-land of Simen ('Simen, its Heights and Abysses,' 1925, pp. 86, 201, 212, and photograph opposite p. 108). In general appearance they are like the giant Lobelias of the Central African mountains.

a single specimen, namely *Medon abessinus*, sp. n., and an *Athela* doubtfully referred to *A. euphorbiæ*, sp. n. They were beaten at the same time, in Jem-Jem Forest, from a dead branch containing a nest of *Camponotus (Myrmotrema) carbo* Emery subsp. *honoris* Forel. The former species was certainly, and the latter probably, found in other habitats besides ants' nests, among them dead parts of tree-Euphorbias. But the record may have some value, since occasional visitors in ants' nests may be in process of becoming true myrmecophiles.

Location of Types.—The first set of the material, including the types of the new species, is in the British Museum, and a second set has been kept by Dr. Bernhauer.

Bibliographical References, etc.—In the systematic report authors' names only are added to names of species previously known. Full references will be found in Dr. Bernhauer's 'Catalogue of Staphylinidæ,' Parts I–VI (Coleop. Cat. parts 19, 29, 40, 57, 67, & 82, 1910–1926), and are only given in this paper in the case of a few species described since the publication of the Catalogue.

I am responsible for the translation of the descriptions, and for the localities, altitudes, and bionomical data under each species. All records from August to December refer to 1926, and those for January and February to 1927.

PART II.—SYSTEMATIC. By MAX BERNHAUER.

LISPINUS MONTANUS, sp. n.

This species is very distinct and not to be confused with any known to me, owing to its narrow form, of equal breadth throughout, and the strongly shagreened, dull surface of the body, especially of the prothorax and elytra.

Rust-red, scarcely pubescent, little convex; legs reddish-yellow. Head much narrower than prothorax, broader than long, with two marked little pits between the roots of the antennæ, otherwise weakly arched, rather strongly shagreened, with only feeble sheen and with fine and scanty puncturation. Antennæ short, somewhat thickened towards the apex, the penultimate segments about half as broad again as long. Prothorax almost as broad as elytra, about $\frac{1}{2}$ broader than long, a little narrowed behind, almost imperceptibly depressed in front of the scutellum, with a deep and broad longitudinal impression in front of either hind angle, these impressions reaching forward through the posterior third, with a very narrow longitudinal polished area along the middle line, otherwise strongly shagreened and dull, with rather strong and widely spaced puncturation. Elytra about half as long again as prothorax, much longer than the breadth of the two elytra combined, with a fine longitudinal furrow near the suture, very strongly shagreened, dull, without lustre, set with isolated shallow, very indefinite, extremely fine punctures. Abdomen strongly shagreened, with isolated punctures, less dull than the anterior parts. Length 3.2 mm.

Loc. Jem-Jem Forest, 8,000–9,000 ft., 27–29. ix., 18 ex. (*Scott*).

LISPINUS COOPERI, sp. n.

Resembles *Lispinus usambaricus* Bernh. (Tanganyika Territory) in form, size, and colour, yet certainly differs from that species in the following points :

Body clearly more convex, with the upper side of its anterior part much more evidently and closely shagreened and thence duller ; the little pits on the head between the roots of the antennæ much more distinct and rather deep ; puncturation of head more evident and less scattered ; antennæ stouter, more strongly thickened towards the apex, but with the penultimate segments not more markedly transverse ; prothorax somewhat longer, with the longitudinal impressions in front of the hind angles broader and deeper, and the puncturation rather finer and less sparse ; elytra somewhat longer, much longer than the breadth of the two elytra combined, indistinctly punctured ; abdomen scarcely differing in any essential character. Length 2·5 mm. (abdomen extended).

Loc. Jem-Jem Forest, 8,000 ft. or above, x., 1 ex. (*Omer-Cooper*).

MEGARTHURUS ABESSINUS, sp. n.

Distinguishable at once from *M. africanus* Eichelb., the second species known from Tropical Africa, as the sides of the prothorax are not dentate.

Black, the first segment of the dark antennæ reddish, legs brown ; immaturely coloured examples are yellowish-brown with the head darker, the bases of the antennæ and the legs reddish-yellow. Head strongly transverse, elevated along the middle and with two weak longitudinal impressions, strongly and closely granulate-punctate, dull, the cheeks behind the eyes shortly protuberant. Antennæ elongate, penultimate segments much longer than broad, terminal segment broader, nearly as long as the two preceding together. Prothorax twice as broad as long, broadest in front of its hind margin, and rather broader at that point than the elytra at their base, narrowed in front with feebly arcuate sides, with hind angles truncated obliquely backwards, with sides extremely finely and indistinctly crenulate, with a sharp and deep median groove extending throughout its length, with surface broadly and deeply impressed near the sides, strongly and closely granulate-punctate, rather dull. Elytra twice as long as prothorax, broadened towards the hind end, strongly and closely granulate-punctate, with little lustre. Abdomen matte-shagreened, finely and closely punctured, clothed like the rest of the body with extremely short golden-yellow hairs. Length 2·5 mm.

Loc. Jem-Jem Forest, ca. 9,000 ft., 24. ix. (*Scott*) ; summit of Mt. Chillálo, 12,000 ft. or more, from decaying stem of tree-Lobelia, 21. xi., 1 ex. (*Scott*) ; Mt. Zukwala, in the crater, ca. 9,000 ft., 26. x., 1 ex. (*Omer-Cooper*).

OMALIUM ALGIDUM Fauvel.

Loc. Mt. Zukwala, forest near highest point, ca. 9,600 ft., 25. x., 12 ex. ; Mt. Chillálo, heath-land near summit, 12,000–13,000 ft., from decaying stems of tree-Lobelia, 21. xi., 3 ex. (all *Scott*).

Originally described from Kilimanjaro.

TROGOPHILÆUS NIGRITA Woll.

Loc. Lake Zwai, western shore, ca. 5,000 ft., xi. 1926, 1 ex. ; Lakes of Addas, Hora Keloli, ca. 7,000 ft., 4. xii., 1 ex. (both *Omer-Cooper*).

Very widely spread in the Old World.

TROGOPHILÆUS EXIGUUS Er., var.

Loc. Lake Hora Abjata, marsh near shore, ca. 5,000 ft., 18. xi., 1 ex. (*Omer-Cooper*).

The species to which this example is referred is very widely spread in the Old World.

OXYTELUS (ANOTYLUS) ÆTHIOPS, sp. n.

Very like the South African *O. caffer* Er. in form, size, and colour, but easily distinguished by the much larger head, matte-shagreened surface of the prothorax and elytra, the shorter prothorax, and especially by the head being more depressed in front and the impression on it bounded by a sharp transverse furrow behind.

Black, indistinctly hairy, with a few weak bristle-hairs at the hind end of the body, legs brownish. Head. (♂) broader than prothorax, broadened towards its base ; (♀) rather narrower than prothorax, not broadened towards its base ; uneven, matte-shagreened, with a slight greasy lustre, especially in front, with a short median furrow in the middle of the vertex, the frons strongly depressed, the impression bounded behind and at the sides by sharp furrows and quadrangularly elevated between these ; eyes not large, rather flattened and scarcely prominent, with small facets ; cheeks rounded behind. Antenna thickened towards the apex, penultimate segments almost twice as broad as long. Prothorax somewhat broader than the elytra between the shoulders, more than twice as broad as long, with sides arcuate, rather narrower behind than in front, with hind angles bluntly indicated, surface matte-shagreened and longitudinally striolate, broadly depressed near the sides, and bearing on the disc three rather deep longitudinal furrows, bounded by clearly shining longitudinal keels. Elytra somewhat longer than prothorax, feebly broadened towards the hind extremity, together not quite twice as broad as long, matte-shagreened, strongly (but not very closely) longitudinally granulate-wrinkled. Abdomen shagreened, less dull than the anterior parts, indistinctly punctured. Length 3-3.5 mm

Loc. Mt. Chillálo, ca. 9,000 ft., by sifting humus under forest-trees, 13. xi., 5 ex. (*Scott*).

OXYTELUS BIDENTULUS Fauvel.

Loc. Mt. Chillálo, ca. 10,000 ft., from excreta of cattle and horses, 17. xi., 3 ex. (*Scott*).

Natal.

OXYTELUS FULGIDUS Fauvel.

Loc. Jem-Jem Forest, from the river-bed, ca. 8,000 ft., 2. x., 2 ex.; Mulu, above the Muger valley, from vegetation near streams, ca. 8,000 ft., 18-23. xii., 1 ex.; Douber River, between Debra Libanos and Addis Ababa, ca. 8,500 ft., 5. i., 1 ex.; Lake Haramaiya, from decayed parts of tree-Euphorbia hedge, ca. 6,600 ft., 22. i., 2 ex. (all *Scott*).

Described (1905) from the Zambesi and from Kenya (Naivasha, Nairobi, etc.).

OXYTELUS GRANDIS Epp., var. ?

Loc. Addis Ababa, grounds of the British Legation, ca. 8,000 ft., 8. ix., 1 ex. (*Omer-Cooper*).

The species to which this example is rather doubtfully referred as a small variety is known from West Africa and from Usambara (Tanganyika Territory).

OXYTELUS LAQUEATUS Marsh., var. ?

Loc. Edge of Jem-Jem Forest, ca. 9,000 ft., 4. x., 1 ex. (*Scott*).

Doubtfully determined as a large form of this very widely distributed species, which is known from the Palearctic Region and both North and South America.

OXYTELUS MIRICEPS Fauvel.

Loc. Jem-Jem Forest, from a deeply shady spot, over 8,000 ft., 10. x., 1 ex. (*Scott*); Mt. Chillálo, ca. 10,000 ft., from excreta of cattle and horses (taken together with *O. bidentulus*), 17. xi., 1 ex. (*Scott*). An example from the Serpent Lake, Wouramboulchi, ca. 9,000 ft., 5. x. (*Omer-Cooper*), with prothorax rather differently shaped, is provisionally referred to this species. But *O. miriceps*, as at present understood, is variable, and may prove to include more than one species.

Described from Amani (Tanganyika Territory).

OXYTELUS PICEUS Fauvel.

Loc. Jem-Jem Forest, ca. 8,000 ft., 25-29. ix., 1 ex. (*Scott*).

Palearctic Region.

OXYTELUS PLANUS Fauvel var. *PUNCTULATUS* Bernh.

Loc. Jem-Jem Forest, from the river-bed, ca. 8,000 ft., 2. x., 1 ex. (*Scott*).

O. planus is recorded from Abyssinia, Eritrea (Bogos), and from West and South Africa.

BLEDIUS (s. str.) *LACUSTRIS*, sp. n.

Separable from related species by the sculpture of the prothorax, by its greater length, and by the sexual characters of the ♂.

Brownish-yellow, moderately shining, thinly covered with yellow hairs; head and hind part of elytra vaguely darker. Head rather narrower than prothorax; with large, swollen, coarsely faceted eyes; matte-shagreened,

with isolated punctures, with a quadrangular, sharply delimited impression in front; in ♂ with a strongly elevated, laterally compressed elevation broadly and straightly truncated at the apex, on either side above the eye; in ♀ with a moderately large protuberance, keeled above, on either side in the same place. Prothorax almost as broad as elytra, scarcely broader than long, with rectilinear parallel sides, feebly arcuate and rather strongly narrowed in the posterior third, with a sharp median furrow extending throughout its length, with surface distinctly shagreened, strongly and diffusely punctured in the posterior third, rather strongly and very closely granulate-wrinkled on the front half and especially towards the anterior angles, and much duller in the same part than behind; in ♂, in the middle of the front margin, with a broad process, only slightly narrowed in front, hollowed above, and formed like a keel at the sides. Elytra considerably longer than prothorax, as long as the breadth of the two elytra combined, rather strongly and closely punctured, finely wrinkled between the punctures. Abdomen distinctly reticulate, more shining than the anterior parts, strongly and diffusely punctured. Length 5.3 mm.

Loc. Shores of Lake Hora Abjata, ca. 5,000 ft., 18. xi., 2 ex. (*Omer-Cooper*).

MIMOGONUS FUMATOR Fauvel, var.

Loc. Small stream W. of Mt. Zukwala, ca. 6,000 ft., 30. x., 1 ex. (*Omer-Cooper*).

M. fumator has a very wide distribution, being recorded from the Sunda Islands and New Caledonia, Madagascar, the West Indies and Mexico.

STENUS (s. str.) *ZUKWALANUS*, sp. n.

This species is transitional between those with keeled, and those with unkeeled, tergites, since in it a distinct little keel is usually visible in the middle of the anterior tergites, but is generally much reduced.

In habitus the species is very like the Palearctic *S. ater* Mannh. Grey-black, sparsely set with little, short, golden-yellow hairs, base of the maxillary palpi and the basal third or half of the femora dirty reddish-yellow, tibiae and tarsi yellow-brown. Head much broader than prothorax, as broad as the elytra at the shoulders, rather deeply concave, with no distinct frontal furrows, only very weakly elevated in the middle, coarsely and very closely punctured, dull, only a diminutive spot shining. Eyes strongly protuberant, the interval between them more than twice as broad as their transverse diameter. Antennae little elongate, shorter than head and prothorax together, third segment almost twice as long as second, penultimate segment little longer than broad. Prothorax much narrower than elytra, about $\frac{1}{4}$ longer than broad, much broadened in the middle, at which point it is broadest, feebly sinuate behind the middle, with no median furrow, coarsely and very closely punctured, entirely dull except for a tiny shining spot on either side of the middle. Elytra quadrate, a little longer than the prothorax, as long as the breadth of the two combined, with prominent shoulders, coarsely and very thickly punctured (like the prothorax), entirely dull. Abdomen moderately closely and coarsely punctured,

a little less so behind ; in the middle of the groove on the anterior tergites there is often a rather indistinct longitudinal keel. Length 5-5.5 mm.

In the ♂ the sixth sternite is broad and shallowly excised ; fifth emarginate in the form of a flat arch, broadly depressed along the middle, the impression stopping somewhat angularly at the sides and being thickly clothed with grey hairs ; fourth and third sternites smoothed in front of the middle of the hind margin and more thickly clothed with grey hairs at the sides.

Loc. From a river in the bush-covered plains S.E. of Mt. Zukwala, ca. 6,000 ft., 31. x., 6 ex. (*Omer-Cooper*).

STENUS (s. str.) *OPACULUS*, sp. n.

Differs from *S. zukwalanus* in being only about half the size and in the following points :—

Colour more intensely black, legs lighter, femora to a much greater extent light yellow. Head less coarsely and closely punctured, feebly shining, with a diminutive mirror-like spot in front of the middle, and two fine but distinct longitudinal furrows ; eyes larger, the interval between them is scarcely twice as broad as their transverse diameter when viewed from above, while in *zukwalanus* it appears quite $2\frac{1}{2}$ times as broad. Prothorax rather less closely punctured, less dull, without the two small mirror-like spots. Elytra less strongly and closely punctured, less dull. Abdomen more finely and almost more closely punctured, with the longitudinal carinae on the bases of the tergites more strongly developed. Lastly, the short hairs are not golden-yellow, but silver-white.

The secondary sexual characters are also essentially different from those of *S. zukwalanus*. In the ♂ the sixth sternite is broadly and deeply emarginate behind and the sides of the excision are produced in the form of teeth ; fifth sternite with a shallower, broadly rounded emargination, the excision having sharply dentate sides, in front of this the sternite is broadly and deeply impressed, the sides of the impression having sharp and high keels, without thick long hairs ; the preceding sternites are without special features, yet more strongly punctured than the tergites. Length 4 mm.

Loc. Mulu, above the Muger Valley, ca. 8,000 ft., 18-23. xii. (*Scott*) ; Entoto, ca. 9,000 ft., 16. ix., 1 ex. (*Scott*) ; Mt. Zukwala, forest near highest point of crater, ca. 9,600 ft., 25. x., 1 ex. (*Scott*).

STENUS (s. str.) *FOSSULATUS* Er., var. ?

Loc. Jem-Jem Forest and the edge of the same, ca. 9,000 ft., 1 & 4. x., 2 ex. (*Scott*).

The specimens are referred with some doubt to this European species.

STENUS (*HYPOSTENUS*) *COOPERI*, sp. n.

A species which recalls certain S. American species (e.g., *S. speculifrons* Fauv.), and possesses no near relatives among known African forms. It stands

out by reason of the strong convexity of its body, its small head, and coarse puncturation.

Deep black, shining; anterior part of body sparsely, abdomen rather thickly, clothed with silver-white hairs; antennæ with segments 2-6 reddish-yellow, the individual segments blackened towards the apex. Head not broader than prothorax, with a long and strong median keel, an oblong elevation over the bases of the antennæ, and a small spot shining like a mirror at the hind third of the inner margin of either eye; otherwise the head is strongly and closely punctured. Antennæ fairly short, segment 9 as long as broad, segments 10 and 11 rather longer than broad. Prothorax only about half as long as elytra, about $\frac{1}{4}$ longer than broad, broadest in the middle, with tolerably symmetrically arcuate sides, somewhat more strongly narrowed in front than behind, coarsely and closely punctured, with a rather long broad median keel which shines like a mirror, and near this on either side with a large, and behind it a small mirror-like spot. Elytra much longer than prothorax, considerably longer than the breadth of the two elytra combined, highly convex, with prominent humeral angles, gently rounded at the sides, coarsely and closely punctured. Abdomen much narrower than elytra, stoutly cylindrical, strongly and fairly closely punctured, not shagreened. Length 4 mm.

In the ♂ the sixth sternite has a very deep and narrow triangular excision.

Loc. Banks of Hawash River, W. of Mt. Zukwala, ca. 6,000 ft., 28. xi., 2 ex.; shore of Lake Hora Abjata, ca. 5,000 ft., 22. xi., 1 ex.; and marsh near the same, 18. xi., 1 ex. (all *Omer-Cooper*); Boru Stream, N. of Mt. Chillalo, ca. 7,500 ft., 29. xi., 1 ex. (*Scott*).

STENUS (HYPOSTENUS) SCOTTI, sp. n.

Closely related to the East African *S. angustiventris* Bernh., but easily distinguishable by its shorter prothorax, shorter and less strongly developed elytra, and much less closely punctured abdomen.

Black, shining, thinly clothed with whitish hairs; antennæ up to their darkened clubs, roots of antennæ and femora, all reddish-yellow; apical half of femora, and all the tibiæ and tarsi, blackish. Head broader than prothorax, but distinctly narrower than elytra, strongly and rather closely punctured, with five shining mirror-like marks as in the preceding species. Antennæ short and like those of *S. cooperi*. Prothorax much narrower than elytra, only a little longer than broad, fairly symmetrically rounded at the sides, coarsely, closely, and fairly evenly punctured, with only a small, longitudinal, polished area in the middle line. Elytra much longer than prothorax, somewhat longer than the breadth of the two elytra combined, flatly arcuate at the sides, like the prothorax but considerably more closely punctured. Abdomen not much narrower than elytra, strongly and fairly closely punctured, the puncturation finer and more widely spaced behind. Length 2.8-3 mm.

Loc. Mulu, above Muger Valley, ca. 8,000 ft., 18-23. xii., 1 ex. (*Scott*); Mt. Zukwala, forest near highest point, ca. 9,600 ft., and in the crater, ca. 9,000 ft., x., 2 ex. (*Scott and Omer-Cooper*).

STENUS (HYPOSTENUS) ALTISSIMUS, sp. n.

Closely related to *S. scotti*, but distinguishable at first sight by the bronzy lustre of the anterior parts, the narrower and more slender build, and the coarser and more diffuse puncturation of the much more strongly shining body.

Black, scantily clothed with short grey-white hairs, anterior part of body with a slight bronzy lustre, antennæ dirty yellow with darker clubs, palpi (excepting the extreme apex) and legs light yellow, knees and tarsi darkened. Head broad, not narrower than the elytra at the shoulders, with a broad and high, brightly polished, longitudinal callosity along the middle, the surface somewhat impressed on either side, strongly and diffusely punctured, shining. Eyes very large, the interval between them about twice as wide as their transverse diameter when viewed from above. Antennæ shorter than head and prothorax together, the club-segments only a little longer than broad. Prothorax much narrower than elytra, much longer than broad, strongly and fairly symmetrically broadened in the middle at the sides, coarsely and not very closely punctured, shining. Elytra longer than prothorax, of fairly even breadth throughout, with prominent humeral angles, punctured like the prothorax, but more evenly and rather closer, shining. Abdomen stout, not margined, with a very fine marginal line at the sides of the 7th and 8th tergites only, strongly and diffusely punctured in front, finely and sparsely behind. Legs moderately long. Tarsi with fourth segment deeply bilobed. Length 2.8 mm.

Loc. Mt. Zukwala, forest near the highest point of the crater-rim, about 9,665 ft., 25. x., 1 ex. (*Scott*), and in the crater, ca. 9,000 ft., 26. x., 1 ex. (*Omer-Cooper*).

STENUS (HYPOSTENUS) ROSELLUS Fauv.

Loc. Mt. Zukwala, ca. 9,000 ft., and the forest near the highest point, ca. 9,600 ft., 21-25. x., 2 ex. (*Scott*); stream W. of Zukwala, ca. 6,000 ft., xi., 1 ex. (*Omer-Cooper*).

In the original description this species was recorded from several parts of East and South Africa, and from Abyssinia.

EDAPHUS sp.

Loc. Mt. Chillálo, forest ca. 9,000 ft., 13. xi., by sifting humus under trees, 1 ex. (*Scott*).

The specimen has some points of resemblance with the type of *E. euplectoides* Sharp, a Central-American species, but is clearly distinct.

PÆDERUS ALUTIVENTRIS, sp. n.

This species is extraordinarily like the East African *P. tropicus* Bernh. in form and colouring, as well as in size, but with some attention it is easily separable by the following distinguishing characters:—

Head larger, broader, almost broader than prothorax, of more even breadth, with much less flatly rounded hind angles, much less coarsely and considerably less closely punctured; eyes larger, more convex; cheeks shorter, only about

twice as long as the longitudinal diameter of the eyes viewed from above, while in *P. tropicus* they are three times as long. Antennæ scarcely different from those of *P. tropicus*. Prothorax somewhat broader, with straighter sides, its puncturation scarcely half as strong and considerably more diffuse. Elytra not projecting at the humeral angles as in *P. tropicus*, but rounded off. Abdomen very distinctly shagreened, much duller, only very finely and fairly closely punctured, the punctures scarcely one-third as strong as in *P. tropicus*. Length 11 mm.

Loc. Mt. Chillálo, ca. 9,000 ft., in humus under forest-trees, 12-13. xi., 2 ex. (*Scott*); Jem-Jem Forest, ca. 8,000 ft., ix., 1 ex. (*Scott*).

PÆDERUS ARROWIANUS, sp. n.

Without hind wings, thinly clothed with grey hairs, deep black, elytra bluish-green, prothorax, first four segments of antennæ, bases of maxillary palpi and femora, as well as coxæ, all yellow-red. Easily recognisable among the moderately small species by its coloration.

Head shining, as wide as prothorax, rounded, somewhat longer than broad, fairly strongly and closely punctured (sparsely in front), in the middle and front to a great extent polished. Eyes large, protuberant, cheeks about as long as longitudinal diameter of eyes. Antennæ elongate, penultimate segments almost twice as long as broad. Prothorax almost as broad as elytra, $\frac{1}{4}$ longer than broad, with fairly straight sides, slightly narrowed towards the base, shining, with some fine points in the dorsal series, laterally extremely finely and sparsely, indeed scarcely visibly, punctured and set with isolated stronger punctures. Elytra about $\frac{1}{3}$ shorter than prothorax, as long as the breadth of the two elytra together, strongly broadened towards the hind end, with bluntly rounded humeral angles, strongly and closely punctured, the punctures deep and wrinkled, shining. Abdomen finely shagreened, less shining than the anterior parts, rather finely and diffusely punctured. Length 7.5 mm.

Loc. Mt. Chillálo, from the heath-land above the forest-limit, ca. 10,000 ft., found under burnt logs of the giant heath, *Erica arborea*, 17-19. xi., 12 ex., and 1 ex. from the forest on the same mountain, ca. 9,000 feet. (all *Scott*).

Dedicated to Mr. G. J. Arrow, of the British Museum (Natural History).

PÆDERUS NIGER, sp. n.

Resembles *P. fauveli* Quedf., a species known from North, West, and East Africa, in its unicolorous black body, but distinguishable by the more diffusely punctured, shining head and prothorax, and the much longer, uneven elytra.

Black, unicolorous; clothed with yellowish hairs, the anterior parts diffusely, the elytra and abdomen fairly closely and partly in patches. Head shining, as broad as prothorax, almost regularly hexagonal, with protuberant eyes situated exactly in the middle of its sides, moderately strongly and not closely punctured (more diffusely in front), polished in the middle. Antennæ moderately long, penultimate segments only little longer than broad. Prothorax much narrower than elytra, fairly shining, about $\frac{1}{3}$ longer than broad, strongly

rounded at the sides, broadest just before the middle, almost symmetrically narrowed in front and behind, not strongly, but rather closely and almost evenly, punctured, with an oblong polished area behind the middle. Elytra considerably longer than prothorax, much longer than the breadth of the two elytra together, parallel-sided, impressed near the suture and before the hind margin, with puncturation rather fine, shallow, close and wrinkled, and surface fairly dull. Abdomen very finely and closely punctured, with feeble lustre. Length 4.8–5 mm.

Loc. Mulu, above the Muger Valley, ca. 8,000 ft., from vegetation near a stream, xii., 1 ex.; Douber River, between Debra Libanos and Addis Ababa, ca. 8,500 ft., 5. i., 3 ex.; Jem-Jem Forest, from the river-bed, ca. 8,000 ft., 2. x., 1 ex.; Akaki Ravine, S.E. of Addis Ababa, 6,500–7,000 ft., 17. x., 1 ex. (all *Scott*).

PÆDERUS PARCEPUNCTATUS, sp. n.

Distinguishable at once from the Palearctic *P. rubrothoracicus* Goeze and all related species by the specially diffuse puncturation of the elytra.

Black, prothorax and bases of maxillary palpi red-yellow, bases of antennæ only a little lighter than the rest of the antennæ, anterior parts of body diffusely. abdomen more closely, clothed with grey-white hairs. Head shining, nearly regularly hexagonal, with protuberant eyes situated in the middle of the sides; it is scarcely longer than broad, rather finely and diffusely punctured, with a polished area in the middle. Antennæ rather elongate, penultimate segments almost twice as long as broad. Prothorax much narrower than elytra, nearly $\frac{1}{3}$ longer than broad, convex, with sides strongly and almost symmetrically arcuate, a little more narrowed towards the front than towards the base, broadest somewhat before the middle; shining and (excepting the impunctate middle zone) with fine and scattered, but not deep, puncturation. Elytra much longer than prothorax, parallel-sided, much longer than the breadth of the two elytra together, rather strongly and very diffusely punctured, shining. Abdomen finely and rather closely punctured, with little lustre. Length 5.5–6 mm.

Loc. Mulu, above the Muger Valley, ca. 8,000 ft., from mountain-streams, xii.; Muger Valley, ca. 5,500 ft., xii.; Douber River, between Debra Libanos and Addis Ababa, ca. 8,500 ft., 5. i.; Debra Libanos, ca. 8,000 ft., 2. i.; small stream W. of Mt. Zukwala, ca. 6,000 ft., xi.; 11 ex. (*Scott* and *Omer-Cooper*).

PÆDERUS VIRIDIPENNIS, sp. n.

This species stands out in strong contrast to the other winged species of medium smallness by reason of its coloration and close, coarse, deep puncturation. It can scarcely be confused with any other.

Deep black, shining, elytra gay emerald-green, prothorax, first three antennal segments and bases of the maxillary palpi red-yellow; the whole body diffusely set with black bristles, in addition to which the elytra bear yellow-grey, and the abdomen black, hairs. Head almost broader than long, hexagonal, with

prominent eyes situated rather behind the middle ; it is scarcely as long as broad, to a great extent smooth, but strongly and rather closely punctured near and behind the eyes ; cheeks shorter than the longitudinal diameter of the eyes. Prothorax rather narrower than elytra, only about $\frac{1}{2}$ longer than broad, broadest in the first quarter, strongly rounded in front, towards the base nearly straight-sided and only slightly narrowed, little convex, with a number of rather strong, clearly impressed bristle-punctures near the wide impunctate middle zone. Elytra shining, much longer than prothorax, of even breadth, much longer than the breadth of the two elytra together, with puncturation coarse, deep, and likewise close. Abdomen less shining than the anterior parts, with puncturation moderately strong and close, and distinctly wrinkled. Length 5 mm.

Loc. Serpent Lake, Wouramboulchi, about 9,000 ft., 5. x., 1 ex. (*Omer-Cooper*) ; between Jem-Jem and Wouramboulchi, 8,000–9,000 ft., 30. ix.–1. x., 1 ex. (*Omer-Cooper*).

PÆDERUS CREBREPUNCTATUS Epp.

Loc. Plains N.W. of Lake Zwai, 5,500–6,000 ft., x.–xi., 1 ex. ; Doukam, 6,500–7,000 ft., 20. x., 1 ex. ; Lake Haramaiya, ca. 6,600 ft., from decaying parts of tree-Euphorbia hedge, 22. i., 3 ex. (all *Scott*).

Tropical East Africa.

PÆDERUS DUPLEX Epp.

Loc. Mt. Chillálo, ca. 8,000 ft., 11. xi., 1 ex. (*Scott*).

Described (1895) from the Arussi Galla country (Ganale Guddä), that is, broadly speaking, in the same district as Mt. Chillálo.

PÆDERUS FUSCIPES Curt.

Loc. Mt. Chillálo, from a pond at about 7,000 ft., 7. xi., 3 ex., and from the Boru stream, N. of the same mountain, ca. 7,500 ft., 20. xi., 1 ex. (all *Scott*).

Cosmopolitan.

PÆDERUS RUFOCYANEUS Bernh.

Loc. Hawash River, W. of Mt. Zukwala, ca. 6,000 ft., 29. x., 1 ex. (*Scott*). Described from Tanganyika Territory.

PÆDERUS SABÆUS Er.

Loc. Wouramboulchi, ca. 9,000 ft., 4–7. x., 1 ex. (*Omer-Cooper*) ; Mt. Zukwala, ca. 9,000 ft., 1 ex., and from the forest near the highest point, ca. 9,600 ft., 1 ex., 23–25. x. (*Scott* and *Omer-Cooper*).

Arabia, Africa, Madagascar.

PÆDERUS SCABRIPENNIS Fauvel var. *USTICOLLIS* Fauvel.

Loc. Hawash River, near the bridge W. of Mt. Zukwala, ca. 6,000 ft., 28. xi., 1 ex. (*Omer-Cooper*).

Described from Kilimanjaro.

ASTENUS MODESTUS, sp. n.

Very distinct owing to its unicolorous dark upper side, but approximating in general form to a large example of the Central-European *A. neglectus* Märkel.

Black to pitch-brown, antennæ, palpi, and legs pale yellow, with a number of black bristles on either side of the body, especially on the prothorax. Head considerably broader than prothorax, longer than broad, closely set with shallow umbilicus-like punctures; eyes prominent, cheeks longer than the longitudinal diameter of the eyes. Antennæ moderately elongate, not thickened towards the apex, penultimate segments about half as long again as broad. Prothorax much narrower than elytra, about $\frac{1}{2}$ longer than broad, strongly rounded at the sides, broadest in the anterior third, in front strongly narrowed, towards the base more weakly so and with straighter sides; surface sculptured like the head. Elytra about $\frac{1}{2}$ longer than prothorax, of even breadth, much longer than the breadth of the two together, with puncturation strong, very close, and roughly wrinkled, and hairs yellow-grey. Abdomen somewhat widened towards the hind end, with puncturation moderately strong, rough, and fairly close, somewhat finer and diffuse towards the apex, and hairs yellow-grey. Length 3.5 mm.

Loc. Between Addis Alam and Jem-Jem, 7,000–8,000 ft., 20. ix., 1 ex. (*Scott*); Digalla, Mt. Chillálo, ca. 9,500 ft., 27. xi., 1 ex. (*Scott*).

ASTENUS TROPICUS Bernh.

Loc. Digalla, Mt. Chillálo, ca. 9,500 ft., 27. xi., 1 ex. (*Scott*).

Described from Rhodesia.

STILICUS CLARISSIMUS Bernh.

Loc. Kattere River, N.E. of Lake Zwai, ca. 6,000 ft., 6. xi., 1 ex. (*Scott*).

Originally described from Abyssinia, from material taken by Mr. Gunnar Kristensen, probably near Dire Dawa.

STILICUS RUBELLUS Epp., var. ?

Loc. Jem-Jem Forest, from a deeply shady place, ca. 8,000 ft., 10. x., 1 ex. (*Scott*).

Doubtfully referred to a species described from West Africa.

STILICUS SCHIMPERI Fauvel.

Loc. Mt. Zukwala, forest near the highest point, ca. 9,600 ft., 23. x., 1 ex. (*Scott*); marsh near Lake Hora Abjata, ca. 5,000 ft., 18. xi., 1 ex. (*Omer-Cooper*).

In the original description recorded from several parts of British East Africa (now Kenya), and from Abyssinia.

ACANTHOGLOSSA BREVICOLLIS (Boh.), var.

Loc. Jem-Jem Forest, ca. 8,000 ft., 27–29. ix., 1 ex. (*Omer-Cooper*).

The species was described from South Africa.

MEDON (s. str.) ABESSINUS, sp. n.

Like the Palearctic *M. apicalis* Kr. and related species in general form, but immediately distinguishable by reason of the stronger and relatively wider-spaced puncturation of the head, and the more widely spaced puncturation of prothorax and elytra.

Black, the elytra up to the dark sutural part, the bases and apices of the brownish antennæ, the palpi, the hind margins of the abdominal segments, and the broad apex of the abdomen, yellow-red; clothed with grey-yellow hairs, with some black bristle-hairs. Head as broad as prothorax, of even breadth, as long as broad, rather shining, finely and moderately closely punctured, the punctures sharply impressed. Antennæ cord-like, penultimate segments rather transverse. Prothorax little narrower than elytra, as long as broad, with sides feebly arcuate, somewhat narrowed towards the base, very finely but not very closely punctured, impunctate along the middle, its surface (like that of the head) extremely finely shagreened and rather shining. Elytra much longer than prothorax, of even breadth, much longer than the breadth of the two elytra together, with fine, rather close, and somewhat wrinkled puncturation, and rather shining surface. Abdomen extremely finely and very closely punctured, duller than the anterior parts. Length 4 mm.

Loc. Jem-Jem Forest, 8,000–9,000 ft., 27–29. ix., 4 ex. (*Scott*); one of these specimens was found in the decaying parts of a tree-Euphorbia on 26. ix., another was beaten out of an ants' nest (*Camponotus (Myrmotrema) carbo* Em. subsp. *honoris* Forel) in a dead branch on 29. ix.

MEDON (s. str.) MONTANELLUS, sp. n.

Very like the preceding in form and size, but differs in the following characters:—

Head a little shorter, inconspicuously broadened towards the base, with punctures finer, more widely spaced and not sharply impressed, and surface more strongly shagreened, less shining, rather dull. Prothorax broader, not narrower than elytra, scarcely as long as broad, rather more narrowed towards the base, more strongly shagreened, less shining, with puncturation much finer, more widely spaced and rather indefinite. Elytra rather shorter, only moderately longer than the breadth of the two together, scarcely more finely but considerably more closely punctured. There is hardly any perceptible difference in the sculpture of the abdomen. The coloration is rather darker, the elytra more brownish-red, the apex of the abdomen more dusky-reddish, the antennæ dark rust-red with lighter bases. Length 4–4.3 mm.

♂ with sixth sternite semicircularly excised, fifth sternite likewise with a deep arcuate emargination, on either side of which it is seamed with black along the hind margin.

Loc. Mt. Chillálo, ca. 9,000 ft., found in sifted humus under forest-trees, 13. xi., 6 ex. (*Scott*).

MEDON (LITHOCHARIS) OCHRACEUS Grav.

Loc. Shores of Lake Hora Abjata, ca. 5,000 ft., 22. xi., 3 ex. (*Omer-Cooper*).
Almost world-wide.

MEDON (PSEUDOMEDON) FULVUS Fauvel, var. ?

Loc. Kattere River, N.E. of Lake Zwai, ca. 6,000 ft., 6. xi., 1 ex (*Scott*).

The species, to which this example is referred with some doubt, was described from the Congo.

PERIERPON HEWITTI Bernh.

Loc. S.E. of Lake Zwai, ca. 5,500 ft., 10-13. xi., 1 ex. (*Omer-Cooper*).

S. and E. Africa, and Abyssinia (Harar district).

The genus *Perierpon* Bernh. was erected for this species alone in W. Michaelsen's 'Beiträge zur Kenntnis der Land- und Süßwasserfauna Deutsch-Südwestafrikas,' vol. i, Lief. 3, Coleop. vii, pp. 317-319 (1915). A second species, *P. kristenseni* Bernh., from Abyssinia, was described in Verh. zool.-bot. Ges. Wien, lxxv, p. 294 (1915).

SCOPÆUS PEREGRINUS Fauvel ?

Loc. Jem-Jem Forest, 8,000-9,000 ft., ix., 1 ex. (*Omer-Cooper*).

The species to which this example is, with some reservation, referred was described from Nairobi and Nakuro (Rift Valley).

SCOPÆUS LÆVIGATUS Gyll., var.

Loc. Kattere River, N.E. of Lake Zwai, ca. 6,000 ft., 6. xi., 1 ex. (*Scott*).

S. lævigatus is a European and Mediterranean species.

CRYPTOBIUM ABESSINUM, sp. n.

Very closely related to the East-African *C. nairobiensis* Bernh. (*mixtum* Fauvel *nec* Sharp), but easily distinguished by its larger, rather broader, form, by the prothorax and elytra being shorter and the latter unicolorous.

Black, with grey hairs and little lustre; antennæ and palpi reddish-yellow, middle segments of antennæ more or less darkened at the apex, legs pale yellow with knees blackened. Head narrow, of the same breadth as the prothorax and of even breadth throughout, much longer than broad, strongly and very closely punctured, with the intervals between the punctures not shagreened and the surface shining. The protuberant eyes stand somewhat before the middle of the length; the cheeks are more than twice as long as the longitudinal diameter of the eyes when viewed from above. Antennæ moderately long, first segment rather longer than the four following together, penultimate segments moderately longer than broad. Prothorax considerably narrower than elytra, about $\frac{1}{2}$ longer than broad, of tolerably even breadth, but feebly broadened in the anterior third, narrowed almost imperceptibly behind, rather more strongly at the front margin, with a broad, strongly raised, shining median keel throughout its length, otherwise strongly and

fairly regularly punctured, the punctures almost as close as on the head, with a very small mirror-like spot before the middle, and the intervals not shagreened but clearly shining. Elytra about $\frac{1}{3}$ longer than prothorax, of fairly even breadth, almost imperceptibly rounded at the sides, much longer than the breadth of the two elytra together, but considerably shorter than in *C. nairobiensis*, punctured less strongly than the prothorax, but almost twice as closely, with very slight lustre. Abdomen very finely and very closely punctured, with little lustre. Length 6.9–7.2 mm.

♂: sixth sternite deeply and triangularly excised behind, across nearly its whole breadth; fifth sternite with its hind margin broadly and very shallowly emarginate, and surface deeply concave throughout the whole length of the segment and the width of the emargination, sparsely punctured in the depression and broadly polished before the hind margin; third and second sternites furnished, at a little distance from the hind margin, each with a long transverse line, closely set with short black bristles.

Loc. Mulu, above the Muger Valley, ca. 8,000 ft., from the margin of a mountain-stream, 18–23. xii., 3 ex. (*Scott*).

CRYPTOBIUM UNIFORME, sp. n.

Nearly related to *C. nairobiensis*, but easily distinguished by the absence of yellow colouring at the hind margin of the elytra, the larger and more robust body, and by the head being narrower in proportion to the prothorax.

Pitch-black, with grey hairs and fairly strong lustre; head, especially the hinder half, reddish, antennæ and palpi rust-yellow, the former lighter towards the apex, legs whitish-yellow, knees scarcely darker. Head considerably narrower than prothorax, more than $\frac{1}{3}$ longer than broad, of even breadth behind the eyes and with rounded hind angles, strongly and fairly closely punctured; in front of the middle the punctures are scattered and far apart; surface between the punctures shining, broadly polished at the front margin. Eyes situated just before the middle, moderately convex. Antennæ not thickened towards the apex, slender, with all the segments much longer than broad, and terminal segment about as long as the penultimate. Prothorax much narrower than elytra, about $\frac{1}{3}$ longer than broad, strongly convex, gently rounded at the sides, narrowed in front a little more than behind, with a fairly broad, raised median longitudinal band, coarsely and closely punctured at either side, with a very small and narrow impunctate longitudinal mark before the middle, and surface between the punctures shining. Elytra considerably longer than prothorax, of even breadth throughout, much longer than the breadth of the two elytra together, punctured closely and even more coarsely than the prothorax, moderately shining. Abdomen closely and finely punctured, moderately shining. Length somewhat over 7 mm.

♂: second and third sternites each with a transverse line, closely set with black bristles, in front of the hind margin; sixth sternite feebly bisinuate.

Loc. River S.E. of Mt. Zukwala, ca. 6,000 ft., 31. x., 1 ex. (*Omer-Cooper*).

CRYPTOBIUM NAIROBIENSIS Bernh.

Cryptobium mixtum Fauvel, 1907 (nec Sharp, 1885).*

Loc. Kattere River, N.E. of Lake Zwai, ca. 6,000 ft., 6. xi., 2 ex (Scott); Muger Valley, ca. 5,500 ft., 28-29. xii., 8 ex. (Scott).

Kenya.

CRYPTOBIUM ERRERENSE Bernh.

Loc. Muger Valley, ca. 5,500 ft., 28-29. xii., 1 ex. (Scott).

Known only from Abyssinia; first discovered at Error by Mr. Gunnar Kristensen (Bernhauer, Ann. Mus. Nat. Hungar. xiii, p. 123, 1915).

CRYPTOBIUM ÆTHIOPICUM Bernh., var.

Loc. Stream W. of Mt. Zukwala, ca. 6,000 ft., 27. xi., 1 ex. (Omer-Cooper).

Known only from Abyssinia, where it was discovered by Kristensen in Boroda (Bernhauer, l. c.).

LEPTACINUS MICROPTERUS, sp. n.

Evidently a form inhabiting high mountains; one of the larger species, very distinct by its specially short elytra.

Pitch-brown, with yellow-grey hairs, moderately shining; antennæ rust-yellow to rust-brown, palpi and legs reddish-yellow. Head nearly as broad as prothorax, narrow, elongate, scarcely perceptibly broadened towards the base, much longer than broad, with fine and widely spaced puncturation, a broad impunctate median line, surface clearly shagreened and rather shining, the inner frontal grooves long, not deeply impressed, and converging behind, and the lateral grooves scarcely indicated. Antennæ short, penultimate segments twice as broad as long. Penultimate segment of maxillary palpi strongly widened towards the apex, terminal segment awl-shaped, little shorter than the penultimate. Prothorax elongate, almost imperceptibly narrowed towards the base, about $\frac{1}{2}$ longer than broad, with widely rounded angles, clearly shagreened, rather shining, with about ten strong punctures in the irregular dorsal series, and with a larger number of punctures laterally, a longitudinal group of which on either side forms an irregular series diverging backwards from the dorsal series. Elytra scarcely more than half as long as the prothorax, clearly broadened towards the base, rather depressed, rather strongly and not very closely punctured, with surface extremely finely wrinkled. Abdomen very finely transversely striolate, with puncturation rather fine and very widely spaced, and surface impunctate along the middle line. Length 5.5-7 mm. (the latter, when the abdomen is drawn out).

Loc. Mt. Chillálo, from damp moss on the high heath-land, 12,000-13,000 ft., 21. xi., 15 ex., and from humus under forest-trees, ca. 9,000 ft., 13. xi., 1 ex. (Scott).

* See Bernhauer, Coleopt. Cat., Pars 40 (Staphylinidæ, iii), p. 284 (1912).

LEPTACINUS COOPERI, sp. n.

This species is very like the cosmopolitan *L. parumpunctatus* Gyll. in general form, but smaller and immediately distinguishable by its longer, more closely punctured head and the more closely punctured dorsal series of the prothorax. It is equally easily separable from *L. batychrus* Gyll. by its longer, more diffusely punctured head, much more diffusely punctured elytra, less short antennæ, and especially by the very long and narrow awl-shaped terminal segment of the maxillary palpi.

Pitch-coloured, with lighter elytra and abdomen, the entire antennæ and palpi rust-red, and legs reddish-yellow. Head as broad as the prothorax, about $\frac{1}{3}$ longer than broad, broadened towards the base, rather strongly and moderately closely punctured, broadly polished and shining like a mirror along the median area; the four frontal grooves are long and sharply engraved. Antennæ moderately short, with penultimate segments only about $\frac{1}{2}$ broader than long. Terminal segment of maxillary palpi long and very narrow, only a little shorter than the preceding segment, not broadened towards the base as in *L. batychrus*, but narrow right to the base, where it is scarcely half as broad as the preceding segment. Prothorax scarcely narrower than the elytra, about $\frac{1}{3}$ broader than long, broadest in the first quarter, strongly narrowed towards the base, with about 11 to 12 crowded punctures in the dorsal series, and with a number of punctures on either side, which lie in a series hook-shaped in front and bent backwards. Elytra rather shorter than prothorax, much longer than the breadth of the two elytra together, with rather strong and widely spaced punctures, here and there forming longitudinal series. Abdomen punctured moderately strongly and closely, more finely and more diffusely behind. Length 4.5 mm.

Loc. Hawash Railway Station, ca. 3,500 ft., 2. ix., 1 example, which flew to light (*Omer-Cooper*).

LEPTACINUS ABESSINUS, sp. n.

Closely related to *L. batychrus* Gyll., but distinguishable from all forms of that uncommonly variable species by its longer parallel-sided head, much shorter lateral frontal grooves, and prothorax more strongly narrowed behind.

Unicolorous pitchy-black; antennæ rust-yellow with basal segment somewhat suffused with brown, palpi light yellow, legs brown with lighter tarsi. Head almost broader than prothorax, about $\frac{1}{4}$ longer than broad, parallel-sided, scarcely narrowed towards the front, strongly and relatively closely punctured, with the inner frontal furrows sharp, deep and very long, the lateral furrows much shorter and less definite. Antennæ short, middle segments (up to the segments before the last) twice as broad as long, those nearer the apex rather less transverse. Prothorax at the base somewhat narrower than the elytra at their base, about $\frac{1}{3}$ longer than broad, broadest in front, strongly narrowed, but with the nearly rectilinear sides clearly sinuate, towards the base; with about 10 to 12 fine punctures in the dorsal series, and the lateral

parts confusedly punctured. Elytra considerably shorter than prothorax, about $\frac{1}{2}$ longer than the breadth of the two elytra together, broadened towards the hind end, with rather fine and widely spaced punctures, the outer ones particularly in longitudinal series. Abdomen impunctate along the median zone, finely and diffusely punctured laterally. Length 3.8 mm.

Loc. Jem-Jem Forest, 8,000–9,000 ft., ix.–x., 3 examples (*Scott and Omer-Cooper*).

LEPTACINUS ÆTHIOPICUS, sp. n.

Distinguishable at once from the preceding by the head being broadened towards the base, more strongly rounded at the hind angles, and twice as finely punctured above.

Very like *L. batychnus* var. *linearis* Grav. in colouring and size, but distinguishable by the head and prothorax being each longer, narrower and much more finely punctured (while the prothorax has its front corners even more flatly rounded than in *L. othioides* Baudi) and the elytra being shorter, so that I have no doubt about the distinctness of the two species.

Pitchy-black with somewhat lighter elytra; bases of the antennæ pitchy-brown, palpi and legs dark reddish-yellow. Head almost $\frac{1}{2}$ longer than broad, broadened towards the base, with puncturation fine and rather widely spaced. Prothorax almost half as long again as broad, finely and irregularly punctured, the dorsal series having about twelve fine punctures. Elytra considerably shorter than prothorax, with puncturation fine, widely spaced and rather irregular. Abdomen very finely and sparsely punctured. Length (of out-stretched body) somewhat over 4 mm.

Loc. Jem-Jem Forest, 8,000–9,000 ft., ix., 2 ex. (*Omer-Cooper*).

LEPTACINUS BATYCHRUS Gyll.

Loc. Lake Haramaiya, ca. 6,600 ft., from decayed parts of a tree-Euphorbia hedge, 22. i., 1 ex. (*Scott*).

Cosmopolitan.

NUDOBIUS ABESSINUS Bernh.

Loc. Jem-Jem Forest, ca. 8,000 ft., x., 6 ex., including two from decaying parts of a tree-Euphorbia and three from rotten wood (*Scott and Omer-Cooper*).

Known only from Abyssinia, where it was discovered by Kristensen in Boroda (Bernhauer, Ann. Mus. Nat. Hungar. xiii, p. 134, 1915).

NUDOBIUS COLORIVENTRIS Bernh.

Loc. Jem-Jem Forest, 8,000–9,000 ft., x., 1 ex. (*Omer-Cooper*).

Known only from Abyssinia; discovered by Kristensen in Boroda (Bernhauer, l. c.).

XANTHOLINUS (GYROHYPNUS) ABESSINUS, sp. n.

This new species is very like our common European *X. punctulatus* Payk. in form, size and colouring, but is markedly distinguished by its head being shorter,

much more strongly broadened towards the base, and more coarsely and closely punctured, also by the much more widely spaced puncturation of the rest of the body.

Head only little longer than its breadth behind, strongly broadened towards the base, coarsely and fairly closely punctured at the sides and behind, with the polished intervals on the disc proportionately small, and the two median frontal grooves long. Prothorax shorter than in *X. punctulatus*, somewhat more narrowed towards the base, with puncturation coarser and somewhat more widely spaced, and about three punctures in the dorsal series. Elytra with punctures much stronger and more distant from one another, and a broad, polished, longitudinal stripe on either elytron. Abdomen moderately finely and very diffusely punctured. Length 7 mm.

Loc. Mt. Chillálo, ca. 10,000 ft., from excrement of cattle and horses, 17. x., 3 ex. (*Scott*).

XANTHOLINUS PUNCTULATUS Paykull.

Loc. Mt. Chillálo, heath-land ca. 10,000 ft., 17–19. xi., found under a burnt log of *Erica arborea*, 1 ex. (*Scott*); Jem-Jem Forest, ca. 8,000 ft., 27–29. ix., 1 ex. (*Omer-Cooper*).

The specimens are referred to this Palearctic and North American species.

NEOBISNIUS PROCERULUS Grav.

Loc. Kattere River, N.E. of Lake Zwai, ca. 6,000 ft., 6. xi., 1 ex. (*Scott*).

Almost cosmopolitan, and previously recorded from Abyssinia.

ACTOBIUS SCOTTI, sp. n.

A fine insect, almost larger than *A. rivularis* Kiesenw. (described from Greece), from which and all its congeners hitherto described from the Ethiopian Region it is very clearly distinguishable by the particular shortness of its head, and the very sparse and fine puncturation of head and prothorax.

Black; elytra sometimes brownish (in presumably immature examples), antennæ blackish, palpi and legs reddish-yellow, with tibiæ and tarsi darkened to a great extent; abdomen slightly iridescent. Head as broad as prothorax, about $\frac{1}{3}$ broader than long, broadly polished along the middle, very finely and very diffusely punctured at the sides. Eyes large, rather prominent; cheeks shorter than the longitudinal diameter of the eyes. Antennæ rather short but slender, penultimate segments little longer than broad. Prothorax as broad as elytra, only little longer than broad, rather convex, feebly rounded at the sides, little narrowed towards the base, with about 9 to 10 fine punctures in the dorsal series, finely and sparsely punctured at the sides. Elytra about as long as prothorax, somewhat longer than the breadth of the two elytra together, with puncturation rather fine, somewhat roughly wrinkled and only moderately close, and surface set with greyish-yellow hairs. Abdomen with puncturation very fine, very close in front, much more diffuse behind, and with surface rather thickly clothed with grey hairs. Length 5 mm.

♂: sixth sternite feebly sinuate in the middle of its hind margin.

Loc. Mt. Chillálo, ca. 9,000 ft., in humus under forest-trees, 13. xi., 1 ex. (*Scott*); Jem-Jem Forest, 8,000–9,000 ft., x., 1 ex. (*Omer-Cooper*).

ACTOBIUS SILVATICUS, sp. n.

This has in common with the foregoing species the sparse puncturation of the anterior part of the body and the broad, even if not quite so short, head. But it is easily distinguished by being only half the size, having still larger eyes and shorter cheeks, the head clearly somewhat narrowed towards the base, the antennæ rather shorter and feebly broadened towards the apex, the prothorax of different form, the elytra shorter and closer punctured, and the front part of the body more strongly shining.

Head about $\frac{1}{4}$ broader than long, narrowed behind; cheeks not as long as the longitudinal diameter of the eyes, hind angles of the head more clearly indicated; the broad impunctate median zone is much larger, and the puncturation is sharply impressed only immediately near and behind the eyes. The penultimate antennal segments are, in their broadest aspect, not longer than broad; terminal segment yellow. Prothorax as broad as long, broadest just in front of the rounded hind angles, narrowed continuously, and with almost rectilinear sides, from the broadest part forwards, with puncturation somewhat less sparse than that of the head, the interstitial sculpture (like that on the head) much more delicate and scarcely visible, whence the upper surface shines more strongly. Elytra clearly shorter than in *A. scotti*, similarly punctured but with interstices much less clearly wrinkled and somewhat more strongly shining. In the abdomen scarcely any perceptible difference can be discerned. The two species are very alike in colour; in the examples now before me the elytra are deep black, the legs entirely pitch-brown. Length 7 mm.

Loc. Mt. Chillálo, ca. 9,000 ft., from forest, 12. xi., 1 ex. (*Scott*).

ACTOBIUS SILVESTRIS, sp. n.

Agrees in coloration with the two preceding species, but is somewhat larger than *A. silvaticus*, from which it differs in the following points:—

Head much less short, only moderately broader than long, almost imperceptibly narrowed towards the base, strongly and rather closely punctured on either side of the polished median zone; eyes more strongly convex, cheeks behind the eyes almost as long as the longitudinal diameter of the latter. Antennæ scarcely different in any essential. Prothorax clearly longer than broad, feebly narrowed towards the front end, much less diffusely punctured on either side of the polished median zone. Elytra much longer than in *A. silvaticus*, considerably longer than prothorax, of tolerably even breadth, longer than the breadth of the two elytra together, more finely and much more closely punctured, rather dull. Abdomen also more closely punctured and duller. Length 4–4.2 mm.

Loc. Jem-Jem Forest, from the bed of the Jem-Jem river, ca. 8,000 ft., 2. x., 1 ex. (*Scott*); Wouramboulchi, ca. 9,000 ft., 5. x., 1 ex. (*Omer-Cooper*); Mt. Chillálo, ca. 9,000 ft., from flood-rubbish and moss in mountain-streams, 12–17. xi., 8 ex. (*Scott*).

PHILONTHUS ARROWIANUS, sp. n.

Closely related to *P. interocularis* Bernh. (Abyssinia), but easily distinguished by the longer and rather differently punctured head, the longer prothorax, and the puncturation of the elytra, which is twice as strong but scarcely half as close.

Deep black, shining, only the tarsi rusty-brownish. Head much narrower than prothorax, somewhat longer than broad, almost imperceptibly broadened towards the base and with hind angles bluntly rounded, with four punctures arranged in pairs between the eyes and sometimes with a supplementary puncture towards the middle, with coarse and isolated punctures near the eyes and finer, uneven, moderately diffuse puncturation behind the latter. Eyes rather large, cheeks behind the eyes somewhat longer than their longitudinal diameter. Antennæ elongate, slender, with penultimate segments longer than broad. Prothorax somewhat narrower than elytra, clearly longer than broad, rounded towards the front, with six to eight strong punctures in the dorsal series, and two supplementary punctures between the series behind the middle, and with very isolated punctures at the sides. Elytra much shorter than prothorax, broadened towards the base, considerably shorter than the breadth of the two elytra together, coarsely and diffusely punctured, with a shallow triangular excision in the hind margin. Abdomen punctured finely, in front closely, towards the posterior end much more diffusely, with a clear rainbow-lustre. Length 8-8.5 mm.

♂: sixth sternite very shallowly emarginate at the hind margin.

Loc. Mt. Zukwala, ca. 9,000 ft., 22. x., 1 ex. (*Scott*); Mt. Chillálo, ca. 8,000 ft., 8. xi., 1 ex. (*Scott*).

PHILONTHUS INCOGNITUS, sp. n.

Philonthus incertus Bernh. i. l. (olim, nec Solsky).

Only differs essentially from the cosmopolitan *P. longicornis* Steph. in its shorter elytra, which are more finely and closely punctured, and in its unicolorous, deep black coxæ and legs. Possibly, with the advent of more material, it will prove later to be a race of that species.* The first antennal segment is also quite black. Length 5 mm.

Loc. Mt. Chillálo, from forest ca. 8,000 ft., also from the heath-land on the summit, 12,000-13,000 ft. (under damp moss and in decaying stem of tree-Lobelia), xi., 3 ex. (*Scott*); Wachacha Ravine, near Addis Ababa, ca. 8,000 ft., ix., 1 ex. (*Scott*); between Jem-Jem and Wouramboulchi, nearly 9,000 ft., ix., 1 ex. (*Omer-Cooper*).

PHILONTHUS SUBÆNEICOLLIS, sp. n.

This characteristic species also stands at all events fairly near *P. longicornis* Steph., but is, however, separable from that and other related species by the

* A form (*kristenseni*, subsp. n.) with short elytra, but doubtless belonging to *P. longicornis*, does occur in Abyssinia (Dire Dawa, *Kristensen*), but it differs from *P. incognitus*, as also does the typical form, in having the elytra more diffusely, and even a trifle more coarsely, punctured.

clear bronzy lustre of its head and prothorax, by the prothoracic series consisting of four punctures, and by the diffusely punctured, strongly iridescent abdomen. In the last character *P. subæneicollis* recalls *P. rudipennis* Fauv., a species described from Kilimanjaro, which also has dorsal prothoracic series of four punctures, but which cannot be confused with the new species, as its abdomen is much more diffusely punctured and the anterior part of its body has no bronzy lustre.

Black; head and prothorax with slight, but always evident, bronzy lustre; legs, including coxæ, pitch-coloured. In the form and puncturation of the head scarcely any essential difference from *P. rudipennis* is discernible, and the antennæ are similarly formed. The head is at the most somewhat shorter, only little longer than broad. The prothorax is somewhat shorter, broader, and more convex, less rounded at the sides, more rectilinearly narrowed towards the front, and scarcely differs in its puncturation. The elytra are much shorter, more coarsely and considerably more diffusely punctured than in *P. rudipennis*, and are much shorter than the prothorax. Abdomen with a strong rainbow-lustre, rather strongly and diffusely punctured, but much less sparsely than in *P. rudipennis*. Length 7.5 mm.

♂: sixth sternite with its hind margin inconspicuously emarginate.

Loc. Mt. Zukwala, ca. 9,000 ft., 21–25. x., 1 ex.; Jem-Jem Forest, 8,000–9,000 ft., ix., 1 ex.; Mt. Chillálo, ca. 9,000 ft., by sifting humus under forest-trees, 13. xi., 1 ex. (all *Scott*).

PHILONTHUS SCOTTI, sp. n.

Resembles *P. methneri* Bernh. (Kilimanjaro) in form and size and in the brilliant purple-golden colour of the elytra, but is at once distinguishable by the strong bronzy lustre of the anterior parts of the body and by the puncturation of the elytra being much finer and closer, while their interstitial surface is wrinkled and dull.

Deep black; head and prothorax with a strong coppery-golden lustre, elytra purple-golden, antennæ and legs dark pitchy-brown, the tarsi lighter, more rusty-yellow. Head somewhat longer than in *P. methneri* Bernh., of more even breadth, with the puncturation on the cheeks and before the hind margin finer and closer, the eyes smaller, the cheeks larger, and the antennæ more elongate, with penultimate segments longer than broad. Prothorax almost as long as broad, moderately narrowed towards the front, with four (or sometimes five) strong punctures in the dorsal series. Elytra nearly as long as prothorax, with puncturation fine, close and wrinkled, and interstices wrinkled and dull. Abdomen finely and closely punctured, scarcely more diffusely behind. Length 12 mm.

Loc. Mt. Chillálo, from forest, ca. 9,000 ft., 15–16. xi., and from heath-land ca. 10,000 ft., 17–19. xi., 2 ex. (*Scott*).

PHILONTHUS (GABRIUS) MONTICOLA, sp. n.

Separable at first sight from *P. katonæ* Bernh. (East Africa), which occurs in

the same faunistic region, by its larger body, different coloration, differently formed head and prothorax, shorter antennæ, and shorter, more closely punctured elytra. A very distinct species, owing to the form of its head and short antennæ.

Black; elytra with a slight bronzy lustre, antennæ and legs brownish, bases of antennæ, palpi, and femora lighter. Head ovate, narrower than prothorax, almost $\frac{1}{3}$ longer than broad, broadened and rounded towards the base, with four punctures approximating to one another in pairs between the eyes, otherwise sparsely and strongly punctured behind the eyes, more finely and closely punctured on the sloping sides and towards the base. Eyes small, cheeks more than three times as long as their longitudinal diameter. Antennæ rather short, second and third segments little longer than broad, middle segments more elongate, penultimate segments scarcely as long as broad. Prothorax somewhat narrower than elytra, about $\frac{1}{4}$ longer than broad, narrowed from the completely rounded-off hind angles forwards and with rectilinear sides, with six strong punctures in the dorsal series and four punctures laterally. Elytra much shorter than prothorax, clearly broadened towards the base, rather strongly and closely punctured, shining. Abdomen finely and moderately closely punctured, shining. Length 5.5–6 mm.

♂: hind margin of sixth sternite broadly emarginate.

Loc. Mt. Zukwala, ca. 9,000 ft., x., 9 ex., including some from forest near the highest point, 9,600 ft.; Mt. Chillálo, ca. 9,000 ft., in humus under forest-trees, 13. xi., 5 ex.; Jem-Jem Forest, ca. 9,000 ft., ix., 1 ex. (all *Scott*).

PHILONTHUS (GABRIUS) MINUTISSIMUS Bernh.

Loc. Jem-Jem Forest, ca. 8,000 ft., ix., 14 ex. (*Omer-Cooper*).

Originally found at Unjanjembe, Tanganyika Territory, in 1911, in cow-dung (see Bernhauer, *Ann. Mus. Nat. Hungar.* xiii, p. 143, 1915).

PHILONTHUS BISIGNATUS Boh.

Loc. Jem-Jem Forest, ca. 8,000 ft., ix., 3 ex. (*Omer-Cooper*).
South Africa.

PHILONTHUS FIMBRIOLATUS Et.

Loc. Same data as the preceding, 1 ex. (*Omer-Cooper*).
Described from Madagascar.

PHILONTHUS LONGICORNIS Steph.

Loc. Serpent Lake, Wouramboulchi, ca. 9,000 ft., 2. x., 1 ex. (*Omer-Cooper*); Mt. Zukwala, ca. 9,000 ft., 21–25. x., 2 ex. (*Scott*); Kattere River, N.E. of Lake Zwai, ca. 6,000 ft., 5. xi., 1 ex. (*Omer-Cooper*).

Cosmopolitan.

PHILONTHUS MARITIMUS Motsch. (?).

Loc. Jem-Jem Forest, 8,000–9,000 ft., x., 1 ex. (*Omer-Cooper*).

The specimen is referred with some doubt to this Mediterranean species.

PHILONTHUS NIGRITULUS Grav.

Loc. Jem-Jem Forest, ca. 8,000 ft., ix., 1 ex., and Serpent Lake, Wouramboulchi, ca. 9,000 ft., 5. x., 1 ex. (*Omer-Cooper*); Mt. Zukwala, ca. 9,000 ft., 21-25. x., 1 ex. (*Scott*).

Cosmopolitan.

ACYLOPHORUS ORIENTALIS Fauvel, var ?

Loc. Jem-Jem Forest, from the river-bed, ca. 8,000 ft., 2. x., 1 ex. (*Scott*).

The species of which this example may be a form was recorded, in the original description, from the Masai steppe near Nairobi and from Kisumu and Kavirondo Bay on Lake Victoria Nyanza.

CONOSOMA ÆTHIOPICUM, sp. n.

Resembles *C. dilutum* Bernh. (Usambara, Tanganyika Territory) in colouring, but is distinguished by its smaller, narrower form, by the antennæ being more strongly broadened towards the apex, by the somewhat finer and more diffuse puncturation, but especially by the absence of bristles at the sides of the elytra.

Reddish-yellow, clothed with yellow hairs; antennæ and legs lighter, the former not darkened in the middle. Head sparsely and indistinctly punctured, shining; antennæ rather strongly broadened towards the apex, with penultimate segments rather strongly transverse. Prothorax moderately broader than long, strongly rounded and narrowed towards the front end, with hind angles rounded off and somewhat produced backwards and surface very finely and diffusely punctured, shining. Elytra little longer than prothorax, distinctly broader than long, without bristle-hairs at the sides, finely and rather closely punctured, with very little lustre. Abdomen very finely and not closely punctured, with black bristles at the sides. Length 1.5 mm.

Loc. Jem-Jem Forest, about 9,000 ft., 1 x., 1 ex.; Mt. Chillálo, from forest, ca. 9,000 ft., 14. xi., 1 ex. (both *Scott*).

CONOSOMA DISCOLOR Bernh., var.

Loc. Kattere River, N.E. of Lake Zwai, ca. 6,000 ft., 5. xi., 1 ex. (*Omer-Cooper*).

Recorded only from Abyssinia, where it was discovered in Boroda by Mr. Kristensen.

Two other examples of this genus, both from Jem-Jem Forest, ca. 8,000 ft., 22-23. ix. (*Scott*), are doubtfully referred to, respectively, *C. nigrosetosum* Bernh., var., and *C. elongatulum* Bernh., var. (immature).

TACHYPORUS COOPERI, sp. n.

This new species stands fairly near *T. silvestris* Bernh. (Tanganyika Territory), but is distinguishable at the first glance by its rather different coloration shorter and duller elytra, and especially by the antennæ, which are quite differently formed, and much longer and more slender.

The reddish-yellow colour on the prothorax is of much narrower extent along the hind margin as well as at the hind angles, and the elytra are pitchy-brown, becoming gradually and indefinitely lighter towards the hind end. The abdominal segments are broadly seamed with reddish-yellow at their hind margins, while in *T. silvestris* they are deep black right to the margin. The difference in the antennæ is also very characteristic: they are not broadened towards the apex as in *T. silvestris*, but are long and slim, with all the segments very elongate, the penultimate ones being still about half as long again as broad. The elytra are moderately longer than the prothorax, very finely and rather closely punctured, and rather closely clothed with grey hairs. The abdomen is very finely and moderately closely punctured, much more diffusely behind. Length 3 mm.

Loc. Jem-Jem Forest, 8,000–9,000 ft., ix., 1 ex.; Mt. Zukwala, ca. 9,000 ft., x., 1 ex. (both *Omer-Cooper*).

TACHYPORUS NITIDULUS Fabr.

Loc. Jem-Jem Forest, 8,000–9,000 ft., ix., 1 ex.; Mt. Zukwala, forest near highest point, ca. 9,600 ft., 23. x., 1 ex.; Mt. Chillálo, forest ca. 9,000 ft., 12. xi., 1 ex. (all *Scott*).

A species distributed throughout the Northern Hemisphere.

COPROPORUS LIVIDIPENNIS, sp. n.

Closely related to *C. gracilicornis* Bernh., 1928 (Congo), by its elongate slender antennæ and the flattened form of its body, but distinguishable at a glance by its yellow elytra, which, moreover, are much longer.

Black, shining as though varnished; elytra, bases of antennæ, palpi and legs reddish-yellow. Head strongly shining, with extremely delicate and sparse puncturation, only visible with difficulty. Antennæ very long and slender, not thickened towards the apex, with penultimate segments much longer than broad. Prothorax as broad as elytra, almost half as broad again as long, rounded at the sides, moderately narrowed towards the front, strongly shining, extremely delicately, indeed scarcely visibly, punctured. Elytra much longer than prothorax, almost longer than the breadth of the two elytra together, almost without any visible sculpture, smooth, narrowly and shallowly grooved near the side-margins. Abdomen finely and diffusely punctured. Length 2–2.5 mm.

Loc. Jem-Jem Forest, ca. 9,000 ft., 6 ex., including 3 from beneath the bark of a decaying *Mimosa*, 1. x.; also 1 ex. from decaying parts of a tree-*Euphorbia* in the same forest, ca. 8,000 ft., 5–7. x. (all *Scott*).

COPROPORUS ABESSINUS Bernh.

Loc. Kattere River, N.E. of Lake Zwai, ca. 6,000 ft., 6. xi., 1 ex. (*Scott*).

Known only from Abyssinia, where it was discovered by Mr. Kristensen in the Harar district.

COPROPORUS PINGUIS (Epp.).

Loc. Shore of Lake Hora Abjata, ca. 5,000 ft., 17 & 22. xi., 11 ex. (*Omer-Cooper*).

Described (1895) from the Arussi Galla country (Ganale Guddà)—that is, broadly, in the same region where it has been re-discovered by Mr. Omer-Cooper.

LEUCOPARYPHUS SILPHOIDES L.

Loc. Mt. Zukwala, ca. 9,000 ft., 21–25. x., 1 ex.; Jem-Jem Forest, ca. 8,000 ft., 25–29. ix., 1 ex. (both *Scott*).

Cosmopolitan. The specimen from Zukwala is of the typical form, that from Jem-Jem Forest of the var. *pictus* Er.

HYPOCYPTUS CAPENSIS Redt.

Loc. Jem-Jem Forest, ca. 8,000 ft., 23. ix., 1 ex., and 4 other ex. beaten from trees and bushes at the edge of the forest, ca. 9,000 ft., 4. x. (*Scott*).

South Africa. The five Abyssinian specimens vary much in size, one, labelled as var. “*minor*,” being particularly small.

MYLLÆNA AFRICANA Bernh., var. ?

Loc. Mt. Zukwala, ca. 9,000 ft., x., 1 ex. (*Omer-Cooper*).

The only representative of the genus is a specimen in poor condition. It is doubtfully referred to this species, which was described (1930) from the Congo.

PRONOMÆA CORTICALIS, sp. n.

A very outstanding species, owing to the very close puncturation of the anterior parts of the body, while in contrast thereto the abdomen is diffusely, and posteriorly only sparsely, punctured.

Pitchy-black to pitchy-brown with somewhat lighter elytra; apex of the abdomen reddish, antennæ brownish with base dark reddish-yellow, palpi and legs also dark reddish-yellow; yellow-haired, the abdomen at the sides set with short black bristles. Head rather strongly and closely punctured, with little shine; antennæ rather elongate, second and third segments almost equally long, the following segments not transverse, the penultimate ones feebly so, the terminal segment longer than the two preceding segments together. Prothorax distinctly narrower than elytra, about $\frac{1}{4}$ broader than long, narrowed rather more strongly towards the front than towards the base, broadest in the middle, with a broad median longitudinal impression in the ♂, very finely and closely punctured in the impression, dull, otherwise rather strongly and closely punctured (like the head), with little shine. Elytra about $\frac{1}{3}$ longer than prothorax, strongly emarginate on the inner side of the outer hind angles, with puncturation rough, stronger and less close than that of the prothorax, surface also more shining. Abdomen transversely furrowed at the base of the first three completely free segments, with punctures fine and diffuse, stronger in the transverse furrows, and only quite isolated towards the hind end, and with strongly shining surface. Length 3 mm.

♂: the eighth sternite possesses at its hind margin four little teeth, the middle of which are longer and separated by a broad arcuate emargination.

Loc. Jem-Jem Forest, ca. 9,000 ft., from beneath the bark of a decaying *Mimosa*, 1. x., 1 ex. (*Scott*).

Var. silvatica, nov. In some examples the antennæ are shorter, and the prothorax in the ♂ is little impressed and not dull. I name this form *silvatica*, and leave it to future investigation to decide whether we possibly have to do with a distinct species.

Loc. Jem-Jem Forest, 8,000–9,000 ft., ix., 4 ex. (*Scott*).

OLIGOTA SPECTABILIS, sp. n.

Like our European *O. inflata* Mannerh. in form and colour, but more than twice as large, and differing also in the following points:—

Antennæ more robust and stronger towards the apex, where also they are more symmetrically thickened; their club not sharply separated off, seventh segment little broader than sixth and little narrower than eighth; bases of antennæ lighter reddish-yellow, the light colouring more extended. Prothorax much more diffusely punctured, rather shining. Elytra little shorter than in *O. inflata*, rather shining, and punctured much more strongly, almost roughly and considerably more diffusely. Abdomen more strongly shining, with puncturation distinctly more diffuse. Although the coloration is very similar to that of *O. inflata*, yet the elytra are coloured the same as the rest of the body, namely pitchy-black, and the light colouring of the apex of the abdomen is more extended. Length 1.8 mm.

Loc. Jem-Jem Forest, ca. 8,000 ft., beaten from grass-thatch of hayricks on cultivated ground at the edge of the forest, 6. x., 1 ex. (*Scott*).

OLIGOTA FLAVICORNIS Lac.

Loc. Mt. Zukwala, ca. 9,000 ft., 23. x., 1 ex. (*Scott*).

Recorded from Europe and the Caucasus.

HOMALOTA DENSICOLLIS, sp. n.

Blackish-brown, rather thickly clothed with grey hairs, and with little shine; head darker, apex of abdomen a little lighter, bases of antennæ, palpi, and legs reddish-yellow. Head somewhat narrower than prothorax, of rounded form but transverse, very finely and rather closely punctured, with surface dull-shagreened, more sparsely sculptured and rather shining in front. Eyes rather large, cheeks shorter than their longitudinal diameter, sharply margined beneath. Antennæ rather long, third segment almost longer than second, the following segments as long as broad, the penultimate ones transversely convex, terminal segment somewhat longer than the two preceding together. Prothorax considerably narrower than elytra, about $\frac{1}{2}$ broader than long, rounded and broadened in the first third, rather strongly narrowed and somewhat sinuate towards the base, with blunt hind angles, broadly and vaguely

impressed along the middle line, finely and closely, but roughly, punctured, surface dull-shagreened, the sides turned ventralwards broadly visible in lateral view. Elytra about a full quarter longer than prothorax, rather broader than long, somewhat emarginate at the hind margin within the hind angles, surface dull and punctured like that of the prothorax. Abdomen somewhat narrowed towards the apex, with the first three exposed tergites transversely furrowed at the base, finely and (in the anterior part) closely punctured, rather shining; towards the hind end the puncturation becomes gradually more diffuse, and is rather sparse on the seventh tergite; the sides, especially towards the apex, are set with long eyelash-like hairs. Length 2 mm.

♂: secondary sexual characters unknown.

Loc. Jem-Jem Forest, ca. 8,000 ft., ix.-x., 2 ex., one from decaying parts of a tree-Euphorbia, the other from decaying wood (*Scott*).

HYPSELUSA, gen. nov.

Related to *Silusa* Er., with which it agrees in most characters, but from which it diverges and should certainly be generically separated, owing to its ligula being cleft at the apex, its head being constricted, and the form of its mesosternum.

Not unlike a small *Bolitochara* in form. Head scarcely narrower than prothorax, transverse, constricted behind, the neck about half as broad as the head, the cheeks not margined beneath. Antennæ rather short, rather strongly thickened towards the apex, with third segment as long as second and the following segments transverse, gradually gaining in breadth, penultimate segments twice as broad as long, terminal segment longer than the two preceding together. Labrum transverse, twice as broad as long, truncate in front, with rounded front angles. Mandibles strong and short, each with a diminutive little tooth in the middle of its inner margin. Inner lobe of maxillæ narrow, horny, in the apical half set with widely spaced, short, curved, thorn-like teeth, which become longer towards the middle, while behind them the lobe bears long hairs; outer lobe narrow, of even breadth, thickly clothed with hairs on its membranous apex; maxillary palpi four-segmented, slender, third segment little longer than second, moderately thickened towards the apex, terminal segment very narrow, awl-shaped, scarcely half as long as the penultimate. Mentum trapezoidal, moderately deeply emarginate at the front margin; ligula narrow and long, two-lobed at the apex, narrowly cleft in the apical third, reaching a little beyond half the length of the first segment of the labial palpi; the latter are long, two-segmented, bristle-like, the two segments of nearly equal length and the second only very little narrower than the first. Prothorax transverse, much narrower than elytra, with two deep longitudinal furrows, connected by a transverse furrow behind, and the epipleura visible in side-view. Elytra of even breadth, distinctly emarginate at the apex within the outer hind angles. Abdomen of even breadth, with lateral margins strongly elevated, and the first four exposed tergites deeply and

broadly furrowed at the base. Prosternum short in front of the anterior coxæ, between which it projects strongly and angularly. Mesosternum not carinate, mesosternal process reaching backwards almost beyond the middle of the middle coxæ and rather broadly truncate behind, the coxæ being widely separated. Legs not very long; front tarsi four-segmented, first segment somewhat longer than second, terminal segment much longer than the three preceding; middle tarsi four-segmented, the first three segments short, of nearly equal size, terminal segment elongate, longer than the three preceding together; hind tarsi five-segmented, the first four segments not very long, of nearly equal size, terminal segment much shorter than the four preceding together.

Since the mesosternal process is truncate behind, the new genus should be referred to the subtribe *Gyrophænæ*, and is perhaps best placed in the system near the Brazilian genus *Parasilusa* Bernh.

The only species so far known, and thus the type of the genus, was found in the high mountain-forests of Abyssinia.

HYPSELUSA SCOTTI, sp. n.

Shining yellowish-red; head and greater part of elytra somewhat darker; bases and apices of antennæ, palpi and legs reddish-yellow; body thinly covered with yellow hairs. Head transverse, coarsely and rather closely punctured; eyes not very prominent, cheeks longer than their longitudinal diameter. Antennæ as given in the description of the genus. Prothorax much narrower than elytra, about $1\frac{1}{2}$ times as broad as long, broadest in the anterior third, rather strongly and almost rectilinearly narrowed towards the base, with distinctly marked though blunt hind angles, with a long and deep transverse furrow in front of the scutellum, on either side of which arises a deep longitudinal furrow, the two converging and reaching forwards to before the middle; surface rather convex, finely and diffusely punctured, and (like the head) strongly shining. Elytra considerably longer than prothorax, with prominent humeral angles, the two elytra together about $\frac{1}{4}$ broader than long, finely and diffusely punctured, strongly shining. Abdomen strongly and closely punctured in the transverse furrows of the tergites, otherwise scarcely punctured, with surface shining like a mirror. Length 2.5-2.8 mm.

External sexual characters are not known.

Loc. Jem-Jem Forest, 8,000-9,000 ft., ix.-x., 8 ex., including one from decaying parts of a tree-Euphorbia and one from under bark of *Juniperus procera* (Scott); Mt. Zukwala, ca. 9,000 ft., x., 1 ex. (Omer-Cooper).

TOMOXELIA BISULCATA Bernh., var.

Loc. Jem-Jem Forest, 8,000-9,000 ft., x., 1 ex. (Omer-Cooper).

Described (1930) from the Congo.

CARDIOLA CSIKII Bernh..

Loc. Jem-Jem Forest, 8,000-9,000 ft., ix.-x., 2 ex. (Scott and Omer-Cooper).

Described from Tanganyika Territory.

FALAGRIA (MELAGRIA) ABYSSINA, sp. n.

Closely related to the Mediterranean *F. nœvula* Er., but easily distinguishable by its much more diffusely punctured prothorax and elytra, the latter being also much shorter.

Reddish-yellow, shining, thinly clothed with greyish-yellow hairs; head somewhat darkened, elytra, meso- and metasternum more brownish, hind half of abdomen blackish, bases of antennæ and legs lighter reddish-yellow. Head almost as broad as prothorax, rounded but transverse, sparsely and indefinitely punctured, strongly shining. Antennæ short, strongly thickened towards the apex, third segment as long as second, fourth little longer than broad, the following segments becoming gradually broader and shorter, the penultimate ones about $1\frac{1}{2}$ times as broad as long, the terminal segment as long as the two preceding together. Prothorax much narrower than elytra, somewhat broader than long, broadest in the anterior third, strongly rounded towards the front end, rather strongly and rectilinearly narrowed towards the base, with hind angles bluntly rounded off, with a broad and deep groove in front of the scutellum; surface very finely and diffusely punctured, and shining. Elytra scarcely longer than prothorax, much shorter than the breadth of the two together, with prominent but blunt humeral angles; surface very finely and diffusely punctured, shining. Scutellum simply punctured, even. Abdomen with strong transverse impressions at the bases of the first two exposed tergites, finely and not very closely punctured, polished along the hind margins of the tergites. Length 2.2 mm.

Loc. Lakes of Addas, Hora Harsadi, ca. 7,000 ft., 30. xi., 1 ex. (*Omer-Cooper*).

FALAGRIA COARCTICOLLIS Fauvel.

Loc. Jem-Jem Forest, from the river-bed, ca. 8,000 ft., 2. x., 1 ex.; Lake Haramaiya, ca. 6,600 ft., from decaying parts of a Euphorbia-hedge, 22. i., 1 ex. (*Scott*).

Africa, Madagascar, Mascarene Is., Seychelles.

TACHYUSA (ISCHNOPODA) ABYSSINA, sp. n.

Rather smaller than the Palæarctic *T. umbratica* Er., much more shining, with the whole body much more diffusely punctured. The species is, moreover, distinguishable at the first glance by its much narrower prothorax.

Black, with a lively bronzy shimmer, shining, thinly clothed with grey hairs; antennæ blackish-brown, with their bases, as well as the palpi and legs, bright yellow. Head scarcely narrower than prothorax, almost as long as broad, grooved on the frons in the middle line, very finely and moderately closely punctured. Antennæ elongate, slightly thickened towards the apex, with the third segment little shorter than the second, the following segments oblong, the penultimate ones somewhat longer than broad. Prothorax considerably narrower than elytra, scarcely longer than broad, strongly broadened before the middle, rather strongly narrowed and with sides sinuate towards the base,

surface convex, with a very deep longitudinal impression in the middle, and puncturation moderately fine but somewhat rough and close, very fine and diffuse in the impression and towards the front angles, in which places also the surface is shining. Elytra longer than prothorax, with prominent humeral angles, of fairly even breadth, extremely finely and moderately closely punctured. Abdomen of even breadth, rather strongly punctured in the transverse furrows on the third to fifth tergites, otherwise finely, moderately closely and rather evenly punctured. Length 2·2-2·5 mm.

♂: eighth tergite truncate behind, sixth sternite produced, tapering backwards and truncate at hind end.

Loc. Jem-Jem Forest, from the bed of the Jem-Jem river, ca. 8,000 ft., 2. x., 2 ex.; Mt. Chillálo, ca. 9,000 ft., from flood-rubbish or moss in a stream, xi., 1 ex. (*Scott*).

TACHYUSA (ISCHNOPODA) *LONGICOLLIS*, sp. n.

Very like the preceding species in colour, form and size, and only differing in the following points:—

Head not furrowed on the frons, but evenly convex; antennæ somewhat shorter, penultimate segments almost broader than long. Prothorax distinctly longer, somewhat longer than broad, with only a little transverse groove in front of the scutellum, scarcely perceptibly impressed in the middle line, very finely and evenly punctured throughout. Elytra somewhat shorter and more diffusely punctured. Abdomen slightly narrowed towards the base. I have been unable so far to discern any other tangible distinguishing characters. Length. 2·8 mm. (with abdomen extended).

Loc. Jem-Jem Forest, from the bed of the Jem-Jem river, ca. 8,000 ft., 2. x., 3 ex. (*Scott*).

TACHYUSA (ISCHNOPODA) *UMBRATICA* Er., var.

Loc. Jem-Jem Forest, 8,000–9,000 ft., x., 1 ex. (*Omer-Cooper*).

A Palæarctic species, recorded from Europe, Algeria, Tunis and the Caucasus.

AMISCHA *ANALIS* Grav.

Loc. Edge of Jem-Jem Forest, ca. 9,000 ft., 4. x., 1 ex. (*Scott*).

Very widespread; recorded from the Palæarctic Region, N. America and New Zealand.

ATHETA (OREOSTIBA) *SCOTTIANA*, sp. n.

Distinguished by the short elytra, which recall those of the Palæarctic and Indian *A. fungi* Grav., the form of the anterior part of the body and the secondary sexual characters of the ♂, and not to be confused with any known species.

Black, shining, clothed with grey hairs; elytra more blackish-brown, apex of abdomen a little lighter, bases of antennæ and legs reddish-yellow. Head considerably narrower than prothorax, scarcely as long as broad, somewhat broadened towards the hind end, then narrowed again; very finely, indistinctly,

and sparsely punctured, shining; eyes rather small, cheeks much longer than the longitudinal diameter of the eyes seen from above, very finely and indistinctly margined. Antennæ rather short, slender, little thickened towards the apex, third segment very little shorter than second, fourth and following segments slightly transverse, penultimate segments about half as broad again as long, terminal segment somewhat longer than the two preceding together. Prothorax as broad as elytra, about $\frac{1}{3}$ broader than long, evenly rounded at the sides, broadest in the middle, with bluntly rounded hind angles, rather convex on the upper surface, finely and not very closely punctured, shining, only very indistinctly impressed in front of the scutellum. Elytra about $\frac{1}{3}$ shorter than prothorax, with distinctly prominent humeral angles, slightly broadened towards the hind end, not too finely and rather closely punctured, moderately shining. Abdomen of even breadth, transversely furrowed at the bases of tergites 3 to 5, moderately finely and closely punctured, much more diffusely on the seventh tergite, where also it is much more shining. Length 2.5 mm.

♂: eighth tergite truncate behind, sixth sternite strongly produced throughout nearly its whole breadth and broadly truncated at the hind extremity.

Loc. Mt. Chillálo, ca. 9,000 ft., from humus under forest-trees, 13. xi., 2 ex. (Scott).

ATHETA (OUSIPALIA) ALTISSIMA, sp. n.

Easily distinguished from *A. alpicola* Mill. (of the mountains of Central Europe), to which it is very closely related, by its larger, broader form, the stronger convexity of its body, the much longer prothorax, and much longer terminal segment of the antennæ.

Black, moderately shining, clothed with grey hairs; apex of abdomen a little lighter, antennæ rust-brown to rust-red, their terminal segment, as well as the palpi and legs, reddish-yellow. Head small, much narrower than prothorax, strongly broadened towards the hind end, broader than long, very finely, indistinctly and diffusely punctured, shining; eyes very small, cheeks almost three times as long as their longitudinal diameter, not margined beneath. Antennæ short, thickened towards the apex, third segment as long as second, fourth and fifth segments not transverse, the following segments becoming gradually shorter and broader, the penultimate segments half as broad again as long, terminal segment almost as long as the three preceding together. Prothorax as broad as the elytra at the shoulders, at the most $\frac{1}{4}$ broader than long, little rounded at the sides, narrowed a little towards the base, more distinctly towards the front end, with a distinct little furrow in front of the scutellum, not furrowed along the middle line, finely and not very closely punctured, moderately shining, the downward-bent sides clearly visible in lateral view. Elytra half as long as prothorax, considerably broadened towards the hind end, moderately finely and closely punctured, with little shine. Abdomen only clearly transversely furrowed at the base of the first two completely exposed tergites,

finely and not very closely punctured, only very diffusely behind, set with numerous black bristle-hairs, especially in the posterior half. Length 1.8–2 mm.

♂: eighth tergite truncate behind, sixth sternite slightly produced and rounded off.

Loc. Mt. Chillálo, from the high heath-land, ca. 12,000–13,000 ft., taken under damp moss, 21. xi., 6 ex. (*Scott*); Mt. Zukwala, forest near highest point, ca. 9,600 ft., 25. x., 1 ex. (*Scott*).

ATHETA (PHILHYGRA) AMICA, sp. n.

Rather closely related to *A. manyema* Bernh., 1930 (Congo), which it is very like in general form, but easily separable by its broader head, broader, shorter prothorax and different sexual characters. Equally easily separable from *A. sibatwana* Bernh., 1930 (Congo), which has somewhat similar sexual characters, by its size being double, its longer prothorax and much longer, more finely and closely punctured elytra; and from our European *A. palustris* Kiesenw. by its larger head, much longer prothorax and sexual characters.

Pitchy-black, grey-haired, rather shining; elytra lighter or darker brown, legs dirty yellow. Head moderately narrower than prothorax, little broader than long, inconspicuously broadened towards the base, very finely and diffusely punctured, shining; cheeks about as long as the longitudinal diameter of the eyes, very finely margined behind. Antennæ slightly thickened towards the apex, third segment a little shorter than second, the following segments scarcely transverse, progressively broader, the penultimate ones almost $1\frac{1}{2}$ times as broad as long, terminal segment as long as the two foregoing together. Prothorax little narrower than elytra, little (but always distinctly) broader than long, fairly evenly rounded at the sides, very finely but not closely punctured, shining. Elytra considerably longer than prothorax, a little shorter than the breadth of the two combined, slightly broadened towards the hind end, finely and closely punctured, with little shine. Abdomen of rather even breadth, with the first three completely exposed tergites transversely furrowed at the base, punctured finely and rather diffusely, sparsely in the posterior part. Length 2.2–2.5 mm.

♂: seventh tergite with a strong little tubercle in front of the middle of the hind margin, eighth tergite slightly produced in the middle, shallowly emarginate, with the blunt corners of the emargination somewhat thickened.

Loc. Mt. Zukwala, forest near the highest point of the crater-rim, ca. 9,600 ft., 2 ex., and from the floor of the crater (including one beaten from trees), ca. 9,000 ft., x., 3 ex. (*Scott and Omer-Cooper*); Jem-Jem Forest, nearly 9,000 ft., under bark of decaying Mimosa, ix., 1 ex. (*Scott*); Serpent Lake, Wouramboulchi, ca. 9,000 ft., x., 1 ex. (*Omer-Cooper*).

ATHETA (PHILHYGRA) CRATERIS, sp. n.

More than twice as large as *A. (P.) amica* and, moreover, different from that and other related species in that the prothorax is much less shining

and distinctly shagreened, but is, however, not so devoid of lustre as in the subgenus *Traumæcia*. In form *A. crateris* is not unlike a small female of the European *A. granigera* Kiesenw.

Black, with yellowish-grey hairs; elytra brown, antennæ, palpi and legs pitch-coloured. Head small, rounded, indistinctly and sparsely punctured, shining; eyes moderately large, cheeks scarcely longer than their longitudinal diameter, very finely margined beneath and towards the hind end. Antennæ distinctly thickened towards the apex, third segment almost longer than second, penultimate segments about half as broad again as long, terminal segment longer than the two preceding segments together. Prothorax considerably narrower than elytra, only a little broader than long, gently rounded at the sides, scarcely narrowed towards the base, slightly narrowed towards the front, with an indistinct impression in front of the scutellum, extremely finely and sparsely punctured, with the interstitial surface very finely but distinctly shagreened, moderately shining, epipleura visible in lateral view. Elytra about $\frac{1}{4}$ longer than prothorax, somewhat shorter than the breadth of the two together, extremely finely shagreened and, moreover, finely and closely punctured. Abdomen of even breadth, transversely furrowed at the bases of the first three exposed tergites, finely and moderately closely punctured, more diffusely in the posterior part. Length 3.5 mm.

Loc. Mt. Zukwala, in the crater, ca. 9,000 ft., 26. x., 1 ex. (*Omer-Cooper*): Mt. Chillálo, ca. 9,000 ft., by sifting humus in forest, 13. xi., 1 ex. (*Scott*).

ATHETA (s. str.) LOBELIÆ, sp. n.

Very like the European *A. aquatilis* Thoms. in form, colour and size, yet easily distinguishable by its shorter and more closely punctured prothorax, broader head and shorter antennæ, and by the puncturation of the elytra being only half as strong but twice as close.

Black, grey-haired, the anterior part of the body with a dark bronzy lustre; elytra dark brown, bases of antennæ and legs reddish-yellow; sides, especially those of the abdomen, set with a number of black bristles. Head rather narrower than prothorax, transverse, with a small impression on the vertex in the ♂, dull-shagreened, finely and diffusely punctured; cheeks scarcely longer than the longitudinal diameter of the eyes, sharply margined beneath. Antennæ distinctly somewhat thickened towards the apex, third segment rather longer and stouter than second, the following segments not transverse, progressively broader, penultimate segments almost $\frac{1}{2}$ broader than long, terminal segment as long as the two preceding together. Prothorax a little narrower than elytra, about $\frac{1}{2}$ broader than long, little (but fairly evenly) rounded at the sides, a little more narrowed towards the front than towards the base, with an indefinite impression in front of the scutellum, dull-shagreened and, moreover, very finely and rather closely punctured, epipleura distinctly visible in lateral view. Elytra singly about $\frac{1}{4}$ longer than broad, but the two together broader than their length, with prominent shoulders, of even breadth, dull-shagreened, very finely and very closely punctured. Abdomen of even breadth, transversely

furrowed at the bases of tergites 3-5, finely and moderately closely punctured, much more diffusely in the posterior part. Length 3.3-4 mm.

♂: eighth tergite rounded-truncate, sixth sternite moderately produced.

Loc. Mt. Chillálo, from heath-land almost at the summit, 12,000-13,000 ft., taken from the dead stem of a tree-Lobelia, 21. xi., 5 ex. (*Scott*).

ATHETA (s. str.) *EUPHORBIAE*, sp. n.

Somewhat like the widespread African and Oriental *A. dilutipennis* Motsch. in the secondary sexual characters of the ♂, but larger, with the anterior part of the body broader, the breadth of the body more even, the puncturation much closer and rougher and the colouring different. In puncturation it resembles *A. boletophila* Thoms., but is easily distinguishable by the anterior part of the body being broader, its larger size, more convex form, and less short antennæ.

Black, rather dull, with rather thick greyish-yellow hairs, and with only few black bristles at the sides and the apex of the abdomen; clytra lighter or darker yellowish-brown, bases of antennæ, palpi and legs reddish-yellow. Head much narrower than prothorax, transverse, slightly broadened towards the base, shagreened and, moreover, finely, distinctly and rather closely punctured; cheeks scarcely as long as the longitudinal diameter of the eyes, distinctly margined beneath. Antennæ rather slender, little thickened towards the apex, third segment somewhat longer than second, fourth and fifth segments not transverse, the following segments slightly so, penultimate segments scarcely more than about $\frac{1}{2}$ broader than long, terminal segment as long as ninth and tenth together. Prothorax as broad as clytra, about $\frac{1}{2}$ as broad again as long, rounded at the sides, much more strongly narrowed towards the front than towards the base, with an indistinct furrow, quite obsolete in front, along the middle, not very finely, but very closely and distinctly roughly punctured, with the sides turned ventralwards visible in lateral view. Elytra about $\frac{1}{4}$ longer than prothorax, slightly transverse when taken together, punctured like the prothorax. Abdomen not or only slightly narrowed towards the apex, with little shine, transversely furrowed at the bases of the first three exposed tergites, with puncturation moderately fine and very close, becoming gradually more diffuse towards the posterior end, and especially so on the seventh segment, where also it is shining. Length 2.5-3 mm.

♂: eighth tergite armed with four little teeth of equal length and at equal distances apart, the middle two rather blunter than the outer ones; sixth sternite only very little produced, broadly rounded.

Loc. Lake Haramaiya, ca. 6,600 ft., from the decayed parts of a hedge of tree-Euphorbia, 22. i., 21 ex.; Jem-Jem Forest, ca. 8,000 ft., also from decaying parts of tree-Euphorbia, 13 ex.; Mt. Chillálo, heath-land, 12,000-13,000 ft., 18. xi., 1 ex. (all *Scott*).

A single example beaten from the nest of an ant, *Camponotus* (*Myrmotrema*) *carbo* Em. subsp. *honoris* Forel, in a dead branch in Jem-Jem Forest, ca. 8,000 ft., 29. ix., is also doubtfully referred to this species, but is in bad preservation and does not appear to agree very closely with typical specimens.

ATHETA (s. str.) *SCOTTI*, sp. n.

A unicolorous black species of even breadth, which is markedly distinguished by its strongly convex body, its prothorax furrowed along the middle line, and the sexual characters of the ♂. It recalls the European *A. aubei* Bris. in general form.

Deep black, rather shining, with greyish-yellow hairs and widely spaced black bristles towards the posterior end of the body; bases of antennæ, palpi, and legs more pitchy-brown. Head considerably narrower than prothorax, broader than long, inconspicuously broadened towards the base, moderately finely and closely punctured, with interstitial surface extremely finely shagreened, with little shine; cheeks shorter than the longitudinal diameter of the eyes, distinctly margined beneath. Antennæ thickened towards the apex, rather short, third segment as long as second, fourth segment not so, the following segments progressively more distinctly transverse, the penultimate segments about $\frac{1}{2}$ broader than long, terminal segment somewhat longer than the two preceding segments together. Prothorax as broad as elytra, about $\frac{1}{2}$ broader than long, with a distinct little groove in front of the scutellum, which is continued forwards into a distinct median furrow, becoming gradually slighter towards the front; surface rather more finely and closely punctured than the head, indistinctly shagreened; the sides are rounded and narrowed from behind forwards, the hind angles distinctly blunt. Elytra about $\frac{1}{4}$ longer than prothorax, almost as long as the breadth of the two elytra together, somewhat more strongly punctured than the prothorax, but scarcely as closely, with the shagreening of the surface more distinct; epipleura visible in lateral view. Abdomen of even breadth, with the bases of the third to fifth tergites transversely furrowed, moderately finely and closely punctured, more finely and more diffusely in the posterior part. Length 2.5–2.8 mm.

♂: the eighth tergite bears on its hind margin four tiny teeth, of little prominence, the middle two of which project as thickenings over the hind margin, while the lateral teeth, at the angles, are only indistinctly visible.

Loc. Jem-Jem Forest, 8,000–9,000 ft., x., 18 ex., including 8 from decaying parts of tree-Euphorbia, 4 from under bark of decaying Mimosa and other dead wood, and 1 from the river-bed; Mt. Zukwala, forest near the highest point, ca. 9,600 ft., 23. x., 13 ex.; Mt. Chillálo, forest ca. 9,000 ft., 12. xi. (all *Scott*).

ATHETA (s. str.) *HARAMAIYANA*, sp. n.

This species has nearly the broad form of *A. dilutipennis* Motsch. and also rather similar secondary sexual characters, but is, however, easily distinguishable by the following features:—

Head smaller by about $\frac{1}{2}$, of more even breadth, almost broader than the front margin of the prothorax, with smaller eyes and longer cheeks. Antennæ less short, less thickened towards the apex, with their penultimate segments only $\frac{1}{2}$ broader than long. Prothorax less short, not quite $\frac{1}{2}$ broader than long, moderately narrowed towards the front, not narrowed towards the base, with

hind corners rather sharp, yet blunt at the actual angle. Elytra somewhat longer, only a little shorter than the breadth of the two together. Abdomen somewhat more closely punctured. Length 2.2 mm.

♂: eighth tergite furnished with four small, but sharp, little teeth, situated at equal distances apart, of which the middle two are somewhat broader but not thickened, and the lateral ones are not thorn-like.

Loc. Lake Haramaiya, ca. 6,600 ft., from the dead parts of a hedge of tree-Euphorbia, 22. i., 2 ex. (*Scott*).

ATHETA (DATOMICRA) SILVESTRIS, sp. n.

This species must be placed near *A. zostera* Thoms. (Palearctic and N. America), but is double the size and, moreover, easily distinguishable by the much more diffuse puncturation and stronger shine of the body, by its shorter antennæ and elytra, and the different secondary sexual characters of the ♂.

Black, grey-haired, with hind margins of the tergites and apex of the abdomen somewhat lighter, legs reddish-yellow, and bases of antennæ dark. Head considerably narrower than prothorax, slightly broadened towards the base, shining, extremely finely and sparsely punctured; eyes moderately large, flattened, cheeks about as long as the longitudinal diameter of the eyes, margined on the underside towards the posterior end. Antennæ moderately long, distinctly thickened towards the apex, third segment distinctly shorter than second, fourth almost broader than long, the following segments progressively broader and shorter, penultimate segments almost $\frac{1}{2}$ broader than long, terminal segment longer than the two preceding together. Prothorax narrower than elytra between the shoulders, about $\frac{1}{3}$ broader than long, feebly rounded at the sides, only very little narrowed towards the base, rather more so towards the front, with a slight longitudinal impression in front of the scutellum, finely and diffusely punctured, shining, the sides turned ventralwards broadly visible in lateral view. Elytra almost shorter than prothorax, strongly transverse, not sinuate within the hind angles, punctured more strongly than the prothorax and very closely, rather dull. Abdomen distinctly narrowed towards the apex (in some examples, however, of almost even breadth), transversely impressed at the bases of the first three completely exposed tergites, moderately finely and closely punctured, only a little less closely in the posterior part. Length 2.2-2.2 mm.

♂: eighth tergite gently rounded at the hind margin, sixth sternite rather produced, cut off behind in a rather broad curve.

Loc. Jem-Jem Forest, 8,000-9,000 ft., ix.-x., 2 ex., one being from the river-bed (*Scott* and *Omer-Cooper*).

ATHETA (METAXYA) OMERI, sp. n.

This species is rather near the North-European *A. arctica* Thoms., but is easily distinguished, apart from its colouring, by the much shorter

prothorax, stronger puncturation of the anterior part of the body, and longer antennæ.

Parallel-sided, black, grey-haired, rather dull; prothorax and elytra, hind margins of abdominal segments, and apex of abdomen dark yellowish-red, antennæ pitchy-brown, their bases, with the palpi and legs, reddish-yellow. Head half as broad as prothorax, very little broadened towards the base, transverse, finely and not very closely punctured, extremely finely shagreened, scarcely shining; eyes large, twice as long as the cheeks, the latter completely margined beneath. Antennæ elongate, reaching the middle of the elytra when bent backwards, scarcely thickened towards the apex, third segment about $\frac{1}{2}$ longer than second, the following segments longer than broad, penultimate segments in their broadest aspect as long as broad, terminal segment as long as the two preceding together. Prothorax as broad as elytra, about $\frac{1}{2}$ broader than long, strongly rounded at the sides, broadest in the middle, narrowed towards the front somewhat more strongly than towards the base, finely and closely punctured, surface extremely finely shagreened, little shining, the sides bent ventralwards narrowly visible in lateral view. Elytra very little longer than prothorax, together strongly transverse, not emarginate within the outer hind angles, punctured like the prothorax, yet rather more strongly and closely, the part adjacent to the scutellum narrowly brownish. Abdomen of even breadth, transversely furrowed at the bases of the first three exposed tergites, finely and rather closely punctured, much more diffusely in the hind part. Length 3.5 mm. (abdomen rather retracted).

♂: eighth tergite truncate rectilinearly behind, sixth sternite strongly narrowed towards the hind end and produced over the eighth tergite.

Loc. Wouramboulchi (beyond Jem-Jem Forest), from the Serpent Lake, ca. 9,000 ft., 3. x., 3 ex. (*Omer-Cooper*).

ATHETA (COPROTHASSA) PALUDOSA, sp. n.

Nearly of the form of the Palæarctic *A. melanaria* Mannerh., but somewhat broader, and differing from all related species in the unicolorous deep black coloration of the body and the secondary sexual characters of the ♂.

Deep black, little shining, grey-haired, with black bristles at the sides of the abdomen; tibiæ brownish, tarsi reddish. Head moderately narrower than front margin of prothorax, transverse, finely and rather closely punctured; eyes rather large, cheeks little shorter than the longitudinal diameter of the eyes, completely and sharply margined beneath. Antennæ moderately elongate, third segment at least as long as, and in certain aspects appearing somewhat longer than, second, the following segments not transverse, progressively shorter and broader, the penultimate segments at the most about $\frac{1}{3}$ broader than long, terminal segment scarcely as long as the two preceding together. Prothorax almost or quite as broad as elytra, about $\frac{1}{2}$ broader than long, rounded at the sides, with bluntly rounded hind corners, little narrowed towards the

base, somewhat more so towards the front, with a little hollow in front of the scutellum, which in some examples is continued forwards as an indistinct longitudinal furrow, finely and closely punctured, rather dull, the epipleura not visible in lateral view. Elytra about $\frac{1}{4}$ longer than prothorax, of even breadth, distinctly shorter than the breadth of the two elytra together, punctured roughly, and somewhat more strongly, but scarcely more closely, than the prothorax. Abdomen somewhat narrowed posteriorly, finely and closely punctured, somewhat less closely in the posterior part. Length 2.8–3.2 mm.

♂: eighth tergite produced into four sharp little teeth, situated at equal distances apart, sixth sternite somewhat produced and broadly rounded behind.

Loc. Mt. Chillálo, from the heath-land near the summit, 12,000–13,000 ft., 18 & 21. xi., 9 ex., several found on the latter date being from dead stems of tree-Lobelia (*Scott*).

ATHETA (COPROTHASSA) ZUKWALANA, sp. n.

Very distinct owing to the strong and even convexity of the prothorax, which is not very short and rather shining.

Black, grey-haired, the abdomen, moreover, with a number of black bristle-hairs; prothorax often pitchy-brown, elytra lighter or darker brown, hind margins of abdominal segments and apex of abdomen reddish, bases of antennæ, palpi and legs reddish-yellow. Head small, moderately transverse, somewhat broadened towards the base, finely and moderately closely punctured, shining; cheeks shorter than the longitudinal diameter of the eyes, sharply and completely margined beneath. Antennæ little thickened towards the apex, third segment somewhat longer than second, the following segments not transverse, the penultimate ones slightly so, terminal segment somewhat longer than the two foregoing together. Prothorax almost broader than elytra, moderately transverse, scarcely $\frac{1}{3}$ broader than long, broadest just in front of the strong, but distinctly blunt, hind corners, strongly narrowed towards the front, with sides distinctly rounded; surface evenly and strongly convex, without any hollow in front of the scutellum, finely and not very closely punctured, rather shining; epipleura not visible in lateral view. Elytra as long as prothorax, together strongly transverse, distinctly emarginate at the hind margin within the outer hind angles, with roughly wrinkled puncturation, stronger than that of the prothorax and rather close. Abdomen distinctly narrowed towards the hind end, moderately finely and closely punctured, somewhat less closely in the posterior part. Length 2–2.8 mm.

Loc. Mt. Zukwala, near the highest point of the crater-rim, ca. 9,600 ft., 23. x., 13 ex. (*Scott*); Mt. Chillálo, ca. 9,000 ft., from humus under forest-trees, 13. xi., 2 ex. (*Scott*); 1 example from the decaying parts of a tree-Euphorbia in Jem-Jem Forest, ca. 8,000 ft., 26. ix. (*Scott*), is placed with some doubt as a small form of this species.

ATHETA (COPROTHASSA) SUBCANALICULATA, sp. n.

Very like *A. zukwalana*, but differing in the form of the prothorax, which is much shorter, more strongly rounded at the sides, more strongly narrowed towards the base, and distinctly (though sometimes only weakly) furrowed along the middle, and has its hind corners rounded off; the penultimate segments of the antennæ are more strongly transverse, and the elytra are longer and scarcely emarginate within the outer hind angles.

Coloration in general somewhat lighter, prothorax reddish-brown, hind margins of abdominal tergites and apex of abdomen more extensively reddish, antennæ rust-red, their bases, together with the palpi and legs, light reddish-yellow. Prothorax about $\frac{1}{2}$ broader than long, broadest in its posterior $\frac{1}{3}$, strongly rounded at the sides, with hind corners rounded off, with a hollow in front of the scutellum, from which arises a longitudinal furrow, sometimes indistinct and only visible under illumination from a certain direction. Elytra about $\frac{1}{4}$ longer than prothorax. In the form of the abdomen clear differences between the two species are scarcely discernible. Length 2.5 mm.

Loc. Mt. Chillálo, ca. 9,000 ft., from humus under forest-trees, 13. xi., 6 ex., and from Digalla, ca. 9,500 ft., 26. xi., 1 ex. (*Scott*); Mt. Zukwala, forest near the highest point, ca. 9,600 ft., 23. x., 2 ex. (*Scott*), also 1 ex. found in the crater, ca. 9,000 ft., 26. x. (*Omer-Cooper*).

ATHETA (COPROTHASSA) SORDIDA Marsh. (?)

Loc. Mt. Zukwala, ca. 9,000 ft., 21-25. x., 1 ex. (*Scott*).

The specimen is not in good condition and is referred with some reservation to this very widely distributed species.

ÆNICTONIA VOSSELERI Wasm.

Loc. Muger Valley, ca. 5,500 ft., 28-29. xii., 1 ex. (*Scott*).

Described from Tanganyika Territory.

ZYRAS LAMINATUS (Roth).

Loc. Between Jem-Jem Forest and Addis Ababa, 7,000-8,000 ft., 11-14. x., 1 ex., which flew to light in the tent; Doukam, 6,500-7,000 ft., 18. x., 1 ex. (both *Scott*).

Originally described in 1851 from the Province of Tigré, Northern Abyssinia, from specimens obtained by W. Schimper.

ZYRAS NITIDIPENNIS Bernh., var.

Loc. One example flew to light in the tent between Jem-Jem and Addis Ababa, at the same time and place as the specimen of *Z. laminatus* referred to above.

This species was described (1926) from the Congo.

ZYRAS REGALIS Bernh.

Loc. Near Addis Alam (over 20 miles W. of Addis Ababa), ca. 8,000 ft., 18-19. ix., 1 ex. (*Omer-Cooper*). A second specimen (♂), doubtfully referred

to this species as a variety, was taken at the same place and time, on cultivated land (*Scott*).

Originally described from Abyssinia, from a single ♀ collected at Dire Dawa by Mr. Kristensen (Bernhauer, Ann. Mus. Nat. Hungar. xiii, p. 168, 1915).

ALEOCHARA BILINEATA Gyll.

Loc. Mt. Zukwala, ca. 9,000 ft., 21–25. x., 1 ex. (*Scott*).

The single specimen is determined as a small form of this widely distributed European species.

ALEOCHARA BOHEMANI Bernh.

Aleochara rufipes Boheman (nom. præocc.).

Loc. Jem-Jem Forest, nearly 9,000 ft., 24. ix., 1 ex. ; Mt. Zukwala, forest near the highest point, ca. 9,600 ft., 25. x., 1 ex. ; Muger Valley, ca. 5,500 ft., 28–29. xii., 1 ex. (all *Scott*).

South Africa and Tanganyika Territory.

Report on the Brachyura collected in Central America, the Gorgona and Galapagos Islands, by Dr. Crossland on the 'St. George' Expedition to the Pacific, 1924-25. By SUSAN FINNEGAN, B.Sc., Ph.D., F.L.S.

(With 2 Charts and 6 Text-figures.)

[Read 5th February, 1931.]

INTRODUCTION.

The Brachyura dealt with in this paper were collected by Dr. Cyril Crossland on the expedition of the 'St. George' yacht to the South Pacific during the years 1924-25. Most of the material considered here was obtained on the earlier part of the expedition, being collected from the Pacific Shore of the Isthmus of Panama, from the islands in the Bay of Panama and from the Cocos, Gorgona, and Galapagos Islands (Chart I.). A small number of crabs, however, were obtained on the Atlantic side of the Isthmus.

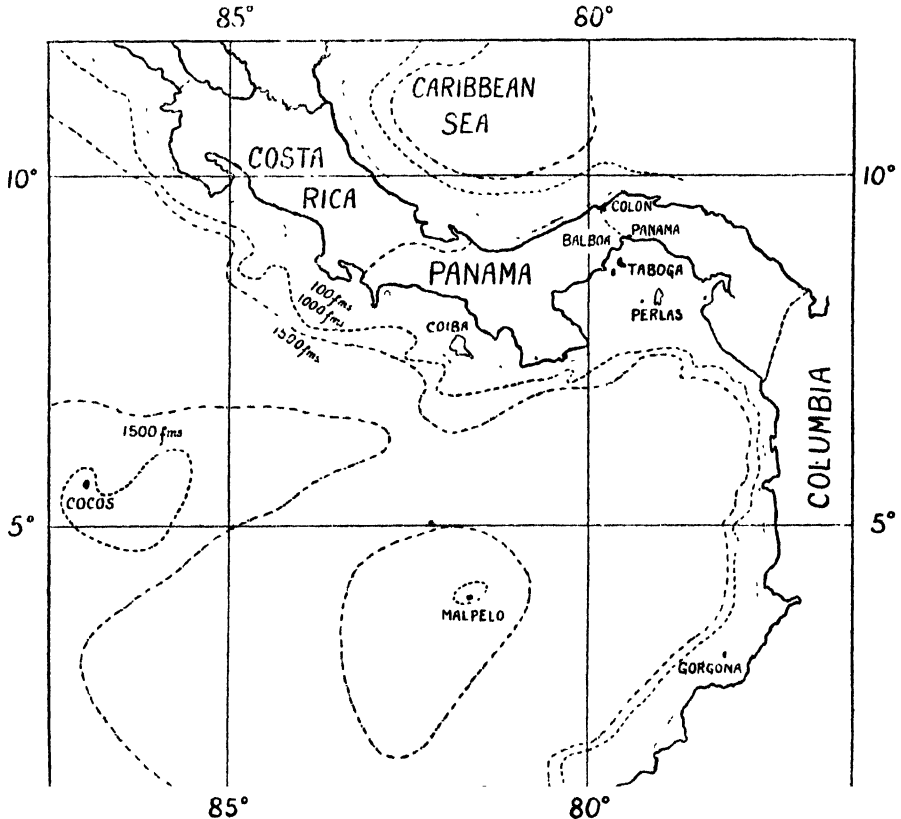
Comparatively little work has been done on the marine carcinological faunas of Central America, particularly on that of the West Coast, although thorough investigations have been undertaken on the fauna of the South-East Coast of the United States and the West Indies. The U.S. Exploring Expedition during the years 1838-42, in which Dana took part, actually covered this ground, but not in great detail. In his report on the Crustacea, Dana dealt very fully with the problem of geographical distribution; but from a systematic standpoint, it is to A. Milne-Edwards's work that we look for the first detailed information on the Crustacean faunas of the East and West Coasts of Central America and their relations to those of surrounding regions.

Subsequent workers in this field of research have been W. Stimpson, S. I. Smith, W. Faxon, A. E. Verrill, and, more recently, M. J. Rathbun, W. L. Schmitt, and Lee Boone. Of these, Faxon has given the most sustained consideration to the characteristic features of this province.

Following on the systematic portion of this paper is a brief discussion on the geographical distribution of the marine Brachyura of this region, particularly in relation to the material collected by Dr. Crossland. The data provided by this collection are supplemented by complete lists of species of Brachyura compiled from all the works on North, South, and Central America (within limits which will be defined) that I have been able to consult personally; they number about two hundred papers. These statistical tables are exceedingly long and have not been printed, but they are accessible in the Zoological Library of the British Museum (Natural History).

The Oxyrhyncha and the Catometopa have been recorded directly from Rathbun's monograph on American species, supplemented in each case from later publications. In this paper Miss Rathbun's classification and nomenclature have been closely followed, as a matter of convenience, in dealing with a region where her numerous and careful writings are our principal sources of information. At the same time I do not wish to be understood as endorsing in every instance the synonymy which she gives, or as accepting her interpretation of the rules of nomenclature.

CHART I.



The Isthmus of Panama and the localities visited by the S.Y. 'St. George.'

The work for this paper was begun in Cambridge University under the supervision of Dr. L. A. Borradaile, and was completed later in the British Museum, where much kind assistance and advice were received from Dr. W. T. Calman, Keeper of the Department of Zoology.

I am indebted also to Miss M. J. Rathbun, Associate in Zoology, United States National Museum, for undertaking the comparison of a specimen with a particular form figured by Hay and Shore, and belonging to the American National Museum at Washington. Dr. Schuchert of Yale University kindly sent me information regarding the geological history of the Antillean Region.

SYSTEMATIC SURVEY OF THE BRACHYURA OF THE
S.Y. 'ST. GEORGE' EXPEDITION.

List of the Species collected by the ' St. George ' Expedition.

Tribe BRACHYURA.

Subtribe OXYSTOMATA.

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Tribe BRACHYURA.

Subtribe OXYSTOMATA.

Family CALAPPIDÆ.

Genus CALAPPA Fabricius.

CALAPPA SAUSSUREI Rathbun. (Text-fig. 1.)

Calappa saussurei Rathbun, Proc. U.S. Nat. Mus. vol. xxi. 1899, p. 609, pl. xli, fig. 6.

Material examined.—Three males from Gorgona.

Habitat.—Shells, dead coral, and gravel overgrown by Polyzoa and *Lithothamnium*.

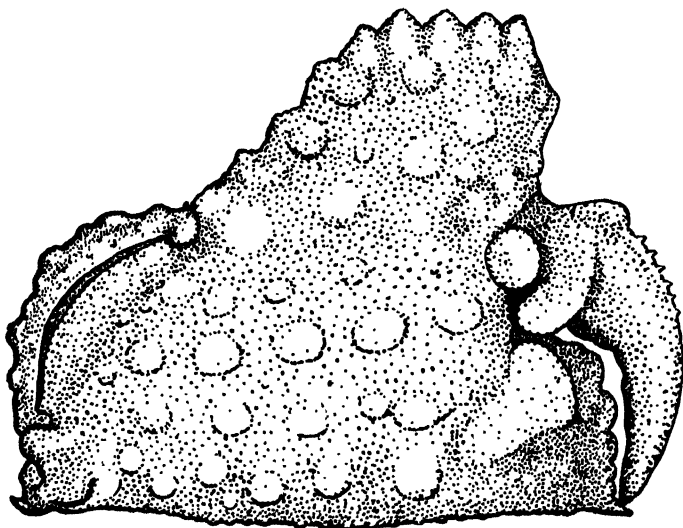
Depth.—15 fathoms.

Remarks.—The specimens from Gorgona differ from Miss Rathbun's description in that the greatest width of the carapace is at the level of the first two

strongly developed teeth of the lateral margin; the lateral margin has four denticles on the hepatic region, and six to eight small denticular teeth on the anterior two-thirds of the branchial region gradually increasing in size; five broad acute teeth follow, but there is more disparity between the small denticular teeth and these five strongly developed teeth than is shown in the figure accompanying the original description of the species. In the three male specimens examined the tubercles on the manus of the cheliped are definitely arranged in rows (text-fig. 1); the tubercles on the carapace show a rough disposition into rows also.

These specimens suggested so close a resemblance to *C. angusta* figured by Hay and Shore (Bull. U.S. Bur. Fish. Washington, vol. xxxv, 1915-1916, pl. xxxi, fig. 7) that I asked Miss Rathbun for her opinion on the matter.

TEXT-FIG. 1.

Cheliped of *Calappa saussurei*, $\times 5$.

The result of her comparisons was that she considers the diagnosis of *C. saussurei* correct; that Hay and Shore photographed by mistake a small *C. flammea*, not the actual specimen of *C. angusta* which she had before her.

Measurements (largest specimen examined was 20.0 mm. long; smallest 8.5 mm. long) :—

	mm.
Length of carapace	20.0
Breadth of carapace at the middle	22.0
Greatest breadth of carapace.....	23.0
Breadth at postero-lateral angles	21.0

Range.—Southern part of the Gulf of California. Recorded now from Gorgona Island.

Genus CYCLOES de Haan.

CYCLOES BAIRDII Stimpson.

Cyclois bairdii Stimpson, Ann. Lyc. Nat. Hist. N.Y. vol. vii, 1862, p. 237; Verrill, Trans. Conn. Acad. Arts Sci. vol. xi, 1901, p. 18, pl. ii, figs. 1, 2.

Cycloes bairdii Rathbun, Proc. U.S. Nat. Mus. vol. xxi, 1899, p. 610.

Material examined.—One male from Gorgona Is. Taken close to the shore.

Habitat.—Among shells, dead coral, and gravel overgrown by Polyzoa and *Lithothamnium*.

Depth.—15 fathoms.

Remarks.—Verrill, in Trans. Conn. Acad. Arts Sci. vol. xiii, 1908, p. 423, distinguishes the Atlantic form taken at Bermuda from those collected in the Pacific, the points of distinction being that in the Atlantic form the carapace is more strongly areolated and appears rougher owing to the relatively larger granules and more elevated tubercles, and that the two frontal teeth are more acute, and have a small lobe or shoulder on the outer edge, while those of the Pacific form are obtuse at the tip and have no lobe.

The carapace has the posterior lateral spines sharper, longer, and farther back, and the sides more rapidly contracted behind the spines. The crests of the chelæ are higher, and the edge more convex, the third tooth from the front being the longest, while in the Pacific form the second tooth is the longest. These teeth are angular or carinate on the front side, but in the Pacific form they are evenly convex. The outer surface of the chelæ has fewer but longer tubercles in the Atlantic form, and the lower edge is bevelled and has two rows of small, rounded, granule-like denticles; these are flatter in the Pacific form. The largest tooth near the lower proximal end is broadly rounded and obtuse in the Atlantic form, acutely triangular in Pacific form.

While most of these characters are relative and cannot be satisfactorily estimated by a comparison of the specimen with the photographs accompanying Verrill's text, the specimen from Gorgona does not completely conform in every respect to those differentiations accorded to the Pacific form. In particular, on the crest of the chelæ, the second tooth from the front is not the longest, but the third, as in Verrill's specimen from Bermuda. Again, the large tooth near the lower proximal end is not acute-triangular, but obtuse. Without having compared actual examples from the Pacific and Atlantic, I have not included *Cycloes bairdii* var. *atlantica* Verrill in the synonymy for this species, but on the results of the examination of the specimen from Gorgona Island I doubt whether it is necessary to form a special variety to receive the Bermuda material.

Measurements :—

	mm.
Length of carapace	14.5
Breadth of carapace	15.0

Range.—California to Panama, Gorgona Is., Bermuda, Porto Rico.

Family LEUCOSIIDÆ.

Genus PERSEPHONA Leach.

PERSEPHONA LICHTENSTEINI Leach. (Text-fig. 2.)

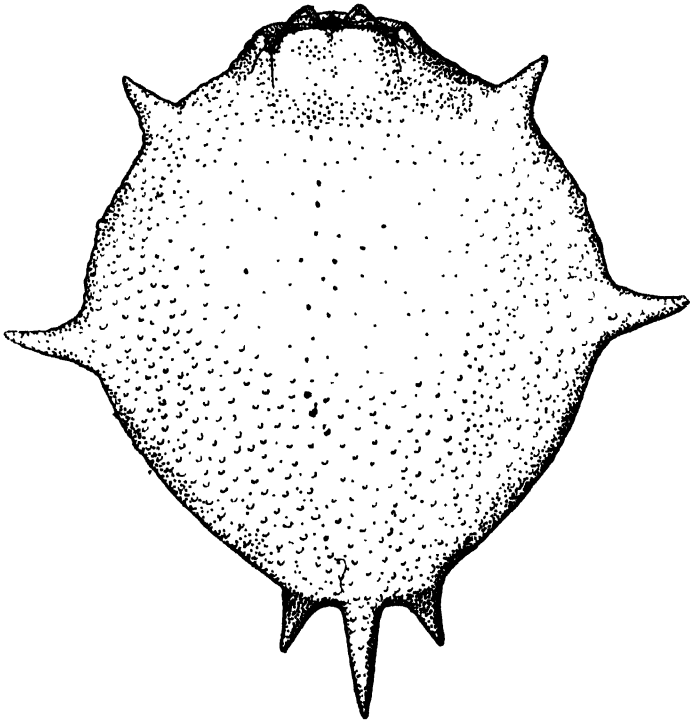
Persephona lichtensteini Leach, Zool. Miscell. vol. iii, 1817, p. 23.

Material examined.—Three males collected by Mr. P. H. Johnson from the Gulf of Paria, Trinidad.

Depth.—3–6 fathoms.

Remarks.—I can find no description of *P. lichtensteini* appearing later than Leach, nor any reference of a locality attached to this species. The following

TEXT-FIG. 2.



Persephona lichtensteini Leach, $\times 6$.

is a description of the specimens examined by me :—Carapace finely punctate, but presenting a smooth shiny surface with no boundaries between the areas marked, although the intestinal region is more pronounced than the rest of the carapace. There are seven long, slender, acute spines distributed one on each hepatic region, one on each branchial region on the margin midway in the length of the carapace, and three posteriorly. The hepatic spines are the shortest of the seven, and are acutely triangular; branchial spines longer, with tips

curving anteriorly; of the posterior spines, two are on the posterior border and are a little longer than the hepatic spines, the third, about one and a half times their length, is standing at a higher level, on the intestinal region. Frontal area with median groove. Exognath of the external maxillipeds slender, showing very little dilatation at the base. No ambulatory legs, and only one cheliped in the material. Merus of the cheliped finely punctate like the carapace, carpus and manus smooth. fingers finely toothed, equal in length to the manus.

Measurements (largest male):—

Length of carapace with median posterior spine	22.0
Length of carapace without median posterior spine	18.0
Breadth of carapace with lateral spines	22.0
Breadth of carapace without lateral spines	16.5

Genus LITHADIA Bell.

LITHADIA CUMINGII Bell.

Lithadia cumingi Bell, Trans. Linn. Soc. vol. xxi, 1855, p. 305, pl. xxxiii, figs. 6-7

Material examined.—One male from Perlas Island, Bay of Panama.

Habitat.—Shells and sand.

Depth.—Dredged from 6-9 fathoms.

Remarks.—The specimen from Perlas Island is older than either figured by Bell, and shows still further confluence of the elevations.

Measurements:—

	mm.
Length of carapace	16.0
Breadth of carapace	16.0

Range.—Lower California, Panama.

Family DORIPPIDÆ.

Genus ETHUSA Roux.

ETHUSA MASCARONE var. AMERICANA (A. Milne-Edwards).

Ethusa americana A. Milne-Edwards, Bull. Mus. Comp. Zool. Harv. vol. viii, no. 1 1880, p. 30; A. Milne-Edwards & Bouvier, Mem. Harv. Mus. Comp. Zool. vol. xxvii, no. 1, 1902, p. 67, pl. xiii, figs. 1-4.

Ethusa mascarone americana Rathbun, Proc. Biol. Soc. Wash. vol. ix, 1897, p. 109; Proc. U.S. Nat. Mus. vol. xxi, 1899, p. 615; Bull. Lab. Nat. Hist. Univ. Iowa, 1898, p. 293.

Ethusa mascarone (pars) Bouvier, Bull. Soc. philom. Paris, ser. 8, T. 9. 1898 p. 65.

Material examined.—One female from Taboga Island, Panama.

Habitat.—From coral fragments overgrown with pink and blue Polyzoa.

Depth.—5 fathoms.

Remarks.—Carapace distinctly granulated, but without the tubercles on the gastric area figured by Milne-Edwards and Bouvier.

Measurements :—

	mm.
Length of carapace	10·0
Breadth of carapace	8·5

Range.—Cape Cod southwards to Gulf of Mexico ; West Indies ; Lower California. Recorded now from Taboga Island, Panama.

ETHUSA MASCARONE var. *PANAMENSIS*, var. *nov.*

Material examined.—Perlas Island, Bay of Panama.

Habitat.—Shell and sand.

Depth.—6–9 fathoms.

Diagnosis.—A variety of *Ethusa mascarone*, with short, forwardly directed, external orbital spines ; with the distance between the tips of the frontal teeth on one side very little less than the distance between the tips of the median pair.

Remarks.—This form differs from *E. mascarone* var. *americana* in the following respects :—

- (a) The shortness of the external orbital spine and its more forward direction. The external orbital spine is shorter than any of the frontal teeth ; in the *americana* variety, the external orbital spine is considerably longer than the frontal teeth.
- (b) Fine granulations occur on the meso- and protogastric areas, but it is not generally granulated on all the protuberances.

From *E. mascarone* var. *hawaiiensis* it differs mostly in :—

- (a) The distances between the teeth on the frontal border—in the *hawaiiensis* variety the distance between the teeth of one side is about a third the distance between the two median teeth.
- (b) Outer orbital tooth more slender than that figured by Miss Rathbun for the Hawaiian specimen.
- (c) The lobules on the cardiac region are not so marked as in the Hawaiian specimen.

From both *Ethusa mascarone* var. *americana* and *E. mascarone* var. *hawaiiensis*, the specimen from Perlas Island is distinguished by the presence of pigment under the more transparent chitin of the carapace, giving it a mottled granular appearance.

Measurements :—

	mm.
Length of carapace	5·0
Breadth of carapace	4·0

Superfamily **Oxyrhyncha**Family **MAJIDÆ**.Genus **STENORYNCHUS** Lamarck.**STENORYNCHUS DEBILIS** (Smith).

Leptopodia debilis Smith, Rep. Peabody Acad. Sci. for 1869–1870, Appendix 1871, p. 87.

Stenorynchus debilis Rathbun, Bull. U.S. Nat. Mus. No. 129, 1925, p. 18, pls. iv–v, text-fig. 4 (full synonymy given here).

Material examined.—Two females and one male from St. Elmo Bay, Perlas Island ; one female and three males from Gorgona Island ; one female and one male from Galapagos Island.

Habitat.—Sand, shells, and dead coral overgrown by Polyzoa and *Lithothamnium*.

Depth.—To 20 fathoms.

Remarks.—After comparing the specimens of *S. debilis* with a great number of specimens of *S. seticornis* from the Atlantic, the only difference that was found was the specific character of the presence of the spine on the basal antennal article of the antennæ, no difference whatever in colour could be detected. These specimens are not bright green with lateral portions of the carapace and also the feet covered with soft grey down, as recorded by Miss Rathbun ; the carapace of one specimen had a pubescent character, but all the others showed the series of brown bands diverging from the median line to the posterior margin and reuniting in front, which is the characteristic colouring for *S. seticornis* also.

Measurements (largest specimen examined, male) :—

	mm.
Length of body	25.0
Length of carapace+rostrum	22.0
Length of carapace to level of the eyes	10.0
Breadth of carapace	9.0
[Smallest male, length	8.0]

Range.—Gulf of California to Panama, Galapagos Islands.

Genus **PODOCHELA** Stimpson.**PODOCHELA ANGULATA**, sp. n.

Material examined.—One female from Gorgona Island.

Habitat.—Shells, dead coral, and gravel overgrown by Polyzoa and *Lithothamnium*.

Diagnosis.—Rostrum thick, subtriangular, not hollow beneath. Propodus of first leg little over twice as long as dactylus. Propodus of last leg very little

longer than dactylus and moderately curved. This diagnosis brings it into line with Rathbun's key of American species and gives it a place closely approximated to *P. macrodera* and *P. grossipes*.

Description.—This species is very closely related to *P. macrodera* and also *P. grossipes*. The body is covered everywhere with a short pubescence, to which foreign particles are attached. The carapace resembles in general shape that of *P. macrodera* very closely; the hepatic region swollen; cardiac region not quite so inflated as gastric region, but bearing a well defined tubercle in the median line just below the two median tubercles of the very much swollen gastric region. Posteriorly, the carapace projects outwards towards the base of the ambulatory legs; this tendency, though quite remarkable, is scarcely as exaggerated as in *P. grossipes*. Merus of outer maxillipede with antero-internal angle very noticeably produced, antero-external angle rounded, merus nearly as broad as ischium. Cheliped of ♀ very slender, manus not dilated, fingers slightly but consistently gaping. There was only one ambulatory leg (the fourth) on the specimen examined, which showed the propodus curved, though not so much as in *P. grossipes*, and the dactylus toothed and biting against the thumb process of the propodus.

This specimen differs from both *P. macrodera* and *P. grossipes* in :—

- (1) The slope of outer maxillipede, the antero-internal angle being more produced than in either.
- (2) The shape of the eyes, which are transversely symmetrical, the cornea coming to a point laterally, not anteriorly.
- (3) The more slender character of the cheliped—this, however, may vary, as only a female specimen was obtained for examination.

From *P. macrodera* this species may be distinguished by the rostrum, which, although the same general shape, is distinctly more pointed. Again, by the presence of *two* tubercles on the gastric region and one on the cardiac region; finally, by the more outward projection of the carapace towards the base of the ambulatory legs.

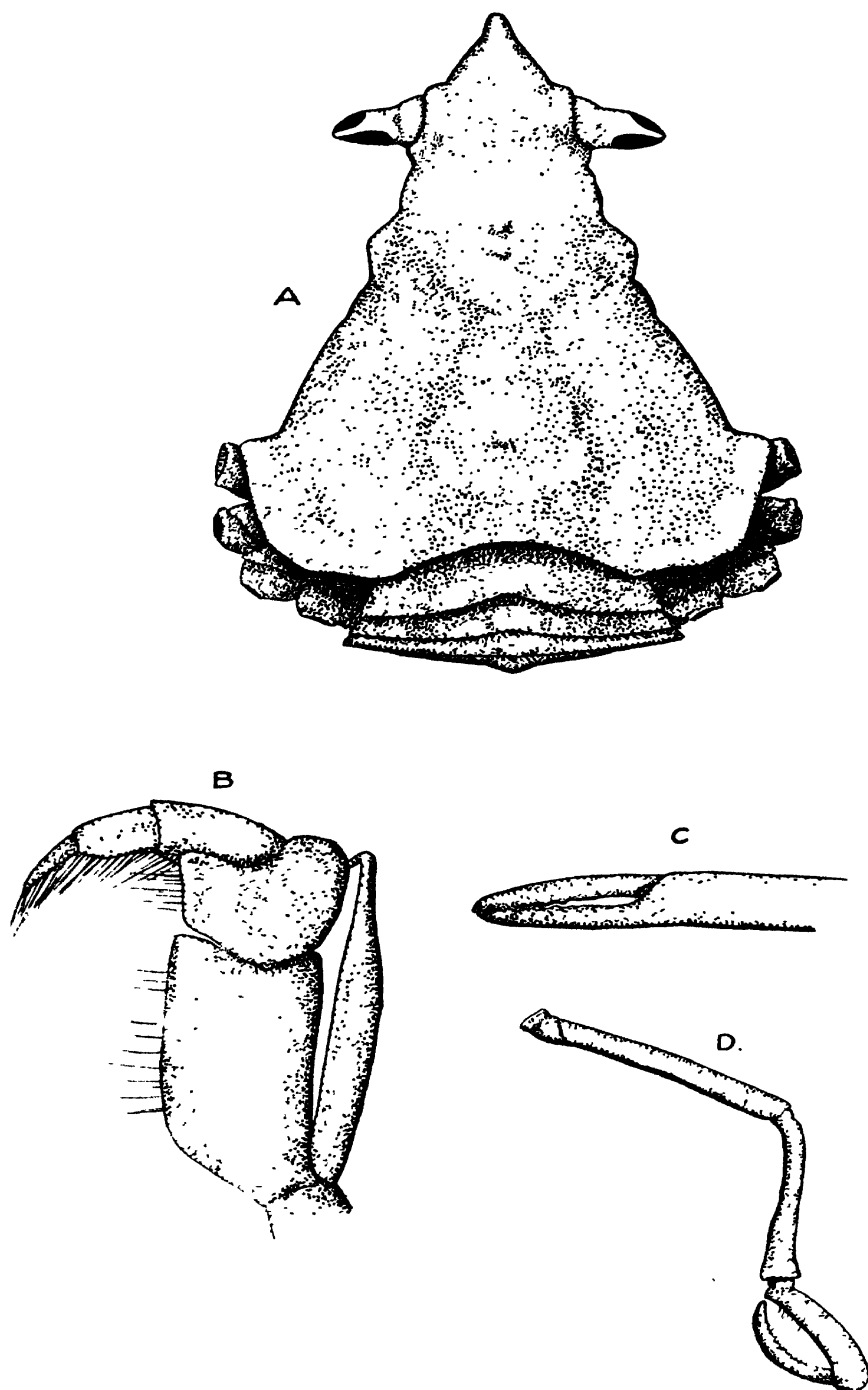
From *P. grossipes* it may be distinguished by the shorter and rather broader rostrum, by the more swollen and tuberculated gastric and cardiac regions, and also by two characters mentioned above in the description of the species, viz. :—the less marked projection of the carapace towards the ambulatory legs and the less strongly curved propodus of the fifth leg. These last two characters are only a matter of degree.

Measurements :—

	mm.
Length of carapace	9
Breadth of carapace	7

Range of Genus.—Coast of middle America from North Carolina to Pernambuco, Brazil, and from San Luis Obispo, California, to the Gulf of California; Galapagos Islands; Bermudas.

TEXT-FIG. 3.



A. *Podochela angulata*, sp. n.
B. Third maxilliped.
C. Chela.
D. Last ambulatory leg.

Genus ACANTHONYX Latreille.

ACANTHONYX PETIVERII H. Milne-Edwards.

Acanthonyx petiverii H. Milne-Edwards, Hist. Nat. Crust. vol. i, 1834, p. 343 ; Rathbun, Bull. U.S. Nat. Mus. No. 129, 1925, p. 142, pls. xlv & ccxxii, figs. 1-6.

Material examined.—Two males from Galapagos Islands, one female and one male from Colon. All young immature forms.

Habitat.—Rocks and sandy shore. Specimens from Colon collected on a coral flat.

Depth.—Shore to 12 fathoms.

Remarks.—Tubercles obsolete. Propodites of ambulatory legs not enlarged. Miss Rathbun after an examination of a large number of specimens considers the absence of these characters due to immaturity. None of the specimens examined were over 5 mm. in length.

Measurements :—

	♂.	mm.
Length of carapace		4.0
Breadth of carapace		3.0
	♀.	
Length of carapace		3.0
Breadth of carapace		2.0

Range.—Common to both sides of the Isthmus. Southern Florida and West Indies to Rio de Janeiro ; Lower California to Valparaiso ; Galapagos Islands.

Genus EPIALTUS.

EPIALTUS PERUVIANUS Rathbun.

Epialtus peruvianus Rathbun, Proc. Biol. Soc. Wash. vol. xxxvi, 1923, p. 72 ; Bull. U.S. Nat. Mus. No. 129, 1925, p. 157, figs. 53, 58.

Material examined.—One female from Post Office Bay, Charles Island, Galapagos.

Depth.—Shore collecting.

Remarks.—The specimen examined is a female, considerably larger than the male described by Miss Rathbun, but agreeing in every detail with the description given. Abdomen with five free articles. Cheliped shorter than first leg.

Measurements :—

	mm.
Length of carapace	7.5
Breadth of carapace	6.0
Length of rostrum	3.5
Length of cheliped	5.5
Length of first leg	6.5

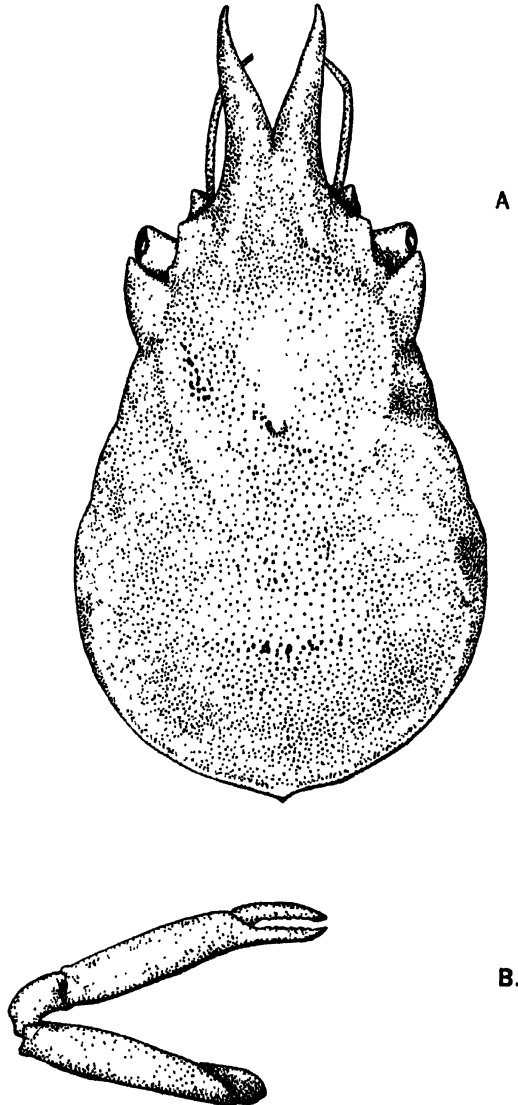
Range.—Chinchas Island, Peru. Recorded now from Galapagos Islands.

Genus *PELIA* Bell.

PELIA ORBICULATA, sp. n. (Text-fig. 4.)

Material examined.—One male from Balboa, Panama.

TEXT-FIG. 4



A. *Pelia orbiculata*, sp. n., $\times 16$.

B. Cheliped of *Pelia orbiculata*, sp. n.

Habitat.—Rocks and rock-pools.

Depth.—At low tide.

Diagnosis.—Carapace high in median line, gastric region higher than cardiac region. Greatest width of carapace not quite two-thirds its greatest length. Rostrum deflexed, rostral horns divergent anteriorly.

The characters which bring this species into line with Miss Rathbun's key to the species of the genus are :—

A. Rostrum not long, one-fifth as long as remainder of carapace.

Basal article of antenna not more than half exposed in dorsal view.

B. Carapace elongated, its greatest width nearly two-thirds its greatest length. Outer margins of rostral horns divergent.

C. Basal article of antenna half exposed in dorsal view.

D. Carapace high in median line, gastric region higher than cardiac

region *orbiculata*, sp. n.

Description.—Body smooth when rough foreign particles are removed. Carapace pyriform; rostrum one-fifth of the remaining length of the carapace, quite as deflexed as in *P. rotunda*, horns divergent anteriorly, incurved at tip. Supraocular cave produced more than in *P. rotunda*, and very much more than in *P. mutica*, with a faint indication of a tubercle at its tip. Orbital border armed with a minute spine. Spine at external angle of basal joint of antennal article as long as in *P. rotunda*. Gastric region of carapace distinctly elevated and surmounted by a small sharp tubercle; cardiac region rounded and smooth, swollen, but not as high as gastric region. The branchial regions are defined anteriorly and flattened somewhat dorsally, and bear on the posterior half two well defined tubercles.

The most distinctive feature of this species is a circular ridge on the carapace, having as its centre the middle point of the cardiac region; it joins the gastric tubercle and the two branchial tubercles, and coincides posteriorly with the hind margin of the carapace, which carries a median tubercle. Cheliped of the female specimen elongate and slender, biting edges of propodus and dactylus finely toothed and close-fitting along their entire length. All the legs with finely reticulate pattern; ambulatory legs with long, sharp, recurved dactyli, the inner margins of which are armed with two rows of setae.

Abdomen of the female with median carina; seven free segments.

This species is close to *P. rotunda* and *P. mutica*, but it may be distinguished from them both by the following characters :—

(a) The rostral horns, although divergent anteriorly, are incurved at the tips.

(b) The very much elevated gastric region.

(c) The peculiar circular ridge and the presence of the four tubercles on the carapace.

Measurements (female) :—

	mm.
Length of carapace along the median line.....	7.5
Length of carapace to end of horns	9.0
Breadth of carapace	5.0

Range of Genus.—Southern Massachusetts to St. Thomas, West Indies ; from Cape St. Roque, Brazil, to northern Patagonia ; from Venice, California, to Panama ; Galapagos Islands.

Genus *HERBSTIA* H. Milne-Edwards.

HERBSTIA TUMIDA (Stimpson).

Herbstiella tumida Stimpson, Ann. Lyc. Nat. Hist. N.Y. vol. x, 1874, p. 95.

Herbstia tumida Rathbun, Bull. U.S. Nat. Mus. No. 129, 1925, p. 299, pl. cv, figs. 5, 6.

Material examined.—One female from Gorgona Island.

Depth.—Shore collecting.

Remarks.—The mesogastric and cardiac protuberances are high and surmounted with a strong tubercle like the female from the Gulf of California ; also the other tubercles of the carapace are quite distinctly present.

Measurements :—

	mm.
Length of carapace	9.5
Breadth of carapace	7.5

Range.—Gulf of California and Manzanilla, Mexico. Recorded now from Gorgona Island.

HERBSTIA EDWARDSII Bell.

Herbstia edwardsii Bell, Proc. Zool. Soc. Lond. vol. iii, 1835, p. 170 ; Trans. Zool. Soc.

Lond. vol. ii, 1836, p. 46, pl. ix, figs. 3, 3 g-3 i ; Rathbun, Bull. U.S. Nat. Mus.

No. 129, 1925, p. 300, pl. cv, figs. 3 & 4, pl. cxxi, figs. 1-4.

Material examined.—One female from Tagus Cove, Albemarle, Galapagos Islands.

Habitat.—Holes in narrow rock-shelf and cave in south side of cove.

Remarks.—The specimen examined shows all the characters noted by Miss Rathbun that distinguished the female collected in St. James's Bay from the type specimen described by Bell.

Measurements :—

	mm.
Length of carapace	7.5
Breadth of carapace	5.5

Range.—Galapagos Islands.

Genus *HEMUS* A. Milne-Edwards.

HEMUS ANALOGUS Rathbun.

Hemus analogus Rathbun, Proc. U.S. Nat. Mus. vol. xxi, 1899, p. 573 ; Bull. U.S. Nat.

Mus. No. 129, 1925, p. 347, pl. cxxiv, figs. 2, 3.

Material examined.—Five females and three males from Taboga Island, Bay of Panama.

Habitat.—Coral fragments overgrown with pink and blue Polyzoa.

Depth.—5 fathoms.

Measurements (largest specimen examined, female, length 7.5 mm., smallest, male, length 5.2 mm.) :—

	mm.
Length of carapace	7.5
Breadth of carapace	7.0

Range.—Southern part of Gulf of California. Recorded now from Taboga Island, Panama.

Genus THOE Bell.

THOE PANAMENSIS Nobili.

Thoe panamensis Nobili, Boll. Mus. Zool. Anat. Comp. Torino, vol. xvi, no. 415, 1901, p. 30; Rathbun, Bull. U.S. Nat. Mus. No. 129, 1925, p. 351, pl. cxxv, figs. 5, 6.

Material examined.—Two males and one female from Gorgona Island.

Measurements (male) :—

	mm.
Length of carapace	9.0
Breadth of carapace	8.0

Range.—Bay of Panama.

Genus PITHO Bell.

PITHO PICTETI (Saussure).

Othonia picteti Saussure, Rev. et Mag. Zool. ser. 2, vol. v, 1853, p. 357, pl. xiii, fig. 2.
Pitho picteti Rathbun, Bull. U.S. Nat. Mus. No. 129, 1925, p. 359, pl. cxxx, figs. 2, 3, pl. cclii, fig. 1.

Material examined.—One young male from Taboga Island, Bay of Panama.

Remarks.—Smaller tubercles on mesogastric region and the three granules forming a curve in front of the cardiac region missing. Cheliped shorter than the length of the carapace.

Measurements (male) :—

	mm.
Length of carapace	8.0
Breadth of carapace	6.5
Length of cheliped	6.0

Range.—West coast of Mexico and Central America.

Genus MITHRAX Latreille.

MITHRAX PYGMÆUS Bell.

Mithrax pygmæus, Bell, Proc. Zool. Soc. Lond. vol. iii, 1835, p. 172; Trans. Zool. Soc. Lond. vol. ii, 1836, p. 55, pl. xi, figs. 3 f–h.

Mithrax (Mithrax) pygmæus Rathbun, Bull. U.S. Nat. Mus. No. 129, p. 406, pl. cclxii, figs. 1–4.

Material examined.—Numerous specimens from Galapagos Islands and Taboga Island, Bay of Panama.

Habitat.—Shore pools. Corals overgrown with pink and blue Polyzoa.

Depth.—From below low water mark to 5 fathoms.

Range.—Panama and Perlas Island. Recorded now from Taboga Island and Galapagos Islands.

Subgenus MITHRACULUS White.

MITHRAX (MITHRACULUS) NODOSUS Bell.

Mithrax nodosus Bell, Proc. Zool. Soc. Lond. vol. iii, 1835, p. 171; Trans. Zool. Soc. Lond. vol. ii, 1836, p. 53, pl. xi, fig. 1.

Mithrax (Mithraculus) nodosus Rathbun, Bull. U.S. Nat. Mus. No. 129, 1925, p. 429, pl. clv.

Material examined.—Two females and one male from the Galapagos Islands.

Habitat.—Shore pool.

Depth.—To 12 fathoms.

Measurements :—

	♂.	mm.
Length of carapace		10.5
Breadth of carapace		12.0
	♀.	
Length of carapace		7.5
Breadth of carapace		8.0

Range.—Galapagos Islands. Chile.

Genus TELEOPHRYS Stimpson.

TELEOPHRYS CRISTULIPES Stimpson.

Teleophrys cristulipes Stimpson, Ann. Lyc. Nat. Hist. N.Y. vol. vii, 1862, p. 190, pl. ii, fig. 2; Rathbun, Bull. U.S. Nat. Mus. No. 129, 1925, p. 441, pl. clix, figs. 1, 2, & 7, pl. cclxii, fig. 7.

Material examined.—Numerous specimens from Galapagos, Gorgona, and Taboga Islands.

Habitat.—Rock pools and among corals.

Depth.—Shore to 12 fathoms.

Remarks.—There is a considerable amount of variation in the numerous specimens of this species collected. The tubercles and the cristate appearance of the legs is much less marked in those collected on the shore than in the specimens taken from corals.

Range.—From Cape St. Lucas, Lower California, to Panama. Recorded now from Galapagos, Gorgona, and Taboga Islands.

Family PARTHENOPIDÆ.

Genus SOLENOLAMBRUS Stimpson.

SOLENOLAMBRUS ARCUATUS Stimpson.

Solenolambus arcuatus Stimpson, Ann. Lyc. Nat. Hist. N.Y. vol. x, 1874, p. 101; Rathbun, Bull. U.S. Nat. Mus. No. 129, 1925, p. 538.

Material examined.—Four females and one young male from the St. Elmo Bay, Perlas Island.

Depth.—6-9 fathoms.

Remarks.—Carpus of cheliped with six denticulated crests, the sixth being very faint. The three crests on the under surface form a Z-shaped figure.

Measurements :—

	♀.	mm.
Length of carapace		10·0
Breadth of carapace		13·5
Length of merus of cheliped		8·0
Length of manus of cheliped		10·0
	Young ♂.	
Length of carapace		7·0
Breadth of carapace		9·0

Range.—Panama.

Genus **LEIOLAMBRUS** A. Milne-Edwards.**LEIOLAMBRUS PUNCTATISSIMUS** (Owen).

Parthenope punctatissima Owen, Zool. of Beechey's Voy. 1839, p. 81, pl. xxiv, fig. 4.

Leiolambrus punctatissimus Rathbun, Bull. U.S. Nat. Mus. No. 129, 1925, p. 543, pl. cxeviii.

Material examined.—One male from Gorgona Island.

Habitat.—Fine sand and small shell-fragments.

Depth.—20 fathoms.

Remarks.—No chelipeds or ambulatory legs are present. Two strong marginal spines are present behind, but the two on the angle of the posterior margin are so very much reduced as to be barely distinguishable at all. Granules distinctly present on the median line of the gastric and cardiac regions. If the chelipeds and ambulatory legs had been present it might have been possible to state definitely whether this should be considered a variety of *L. punctatissimus*.

Measurements :—

	mm.
Length of carapace	10·5
Breadth of carapace—antero-lateral teeth	16·0
Breadth of carapace between antero-lateral teeth	12·5

Range.—Gulf of California ; Mexico ; California (?). Recorded now from Gorgona Island.

Superfamily **Brachyrhyncha**.Family **PORTUNIDÆ**.Genus **PORTUNUS** Fabricius.**PORTUNUS (PORTUNUS) PANAMENSIS** (Stimpson).

Achelous panamensis Stimpson, Ann. Lyc. Nat. Hist. N.Y. 1874, vol. x, p. 112.

Portunus panamensis Rathbun, Proc. U.S. Nat. Mus. vol. xxi, 1899, p. 592.

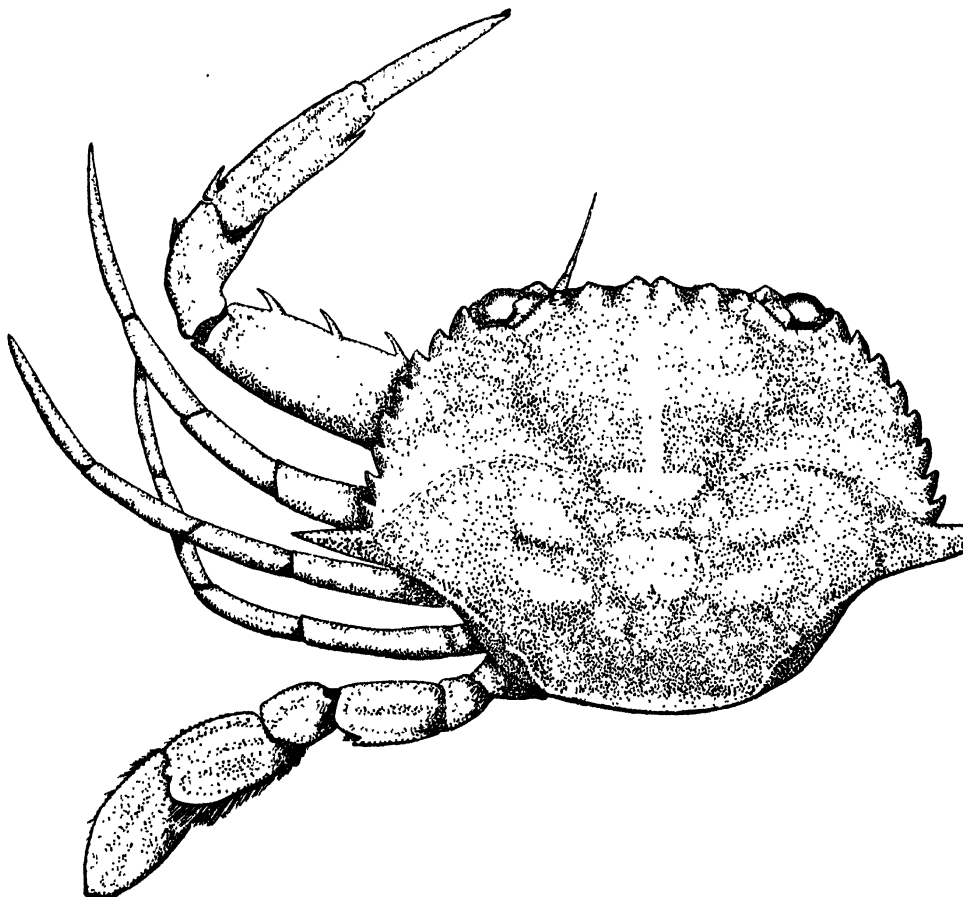
Material examined.—One female and three males from Perlas Island, Bay of Panama.

Habitat.—Shells and sand.

Depth.—6–9 fathoms.

Remarks.—In mature specimens the ninth lateral tooth is equal in length to the space occupied by the preceding teeth. Carpus of cheliped with small external spine in addition to the internal spine; hand armed with two spines, one at articulation with the carpus and the other on the superior carina above the base of the thumb; fingers of the claws overlap.

TEXT-FIG. 5.

*Portunus panamensis* (Stamp.).

Measurements (largest specimen in material a male, length 7.0 mm.; smallest, male, length 5.0 mm.) :—

	mm.
Length of carapace	7.0
Breadth of carapace + lateral spines	14.5
Breadth of carapace between antero-lateral sinuses	11.0
Length of chelipeds	14.0
Ratio of length to breadth 1 : 1.57.	

Range.—Panama Bay.

PORTUNUS (ACHELOUS) SPINIMANUS Latreille.

Portunus spinimanus Latreille, Nouv. Dict. Hist. Nat. vol. xxviii, 1819, p. 47.

Achelous spinimanus Faxon, Mem. Mus. Comp. Zool. Cambridge, Mass. vol. xviii, 1895, p. 23.

Portunus (Achelous) spinimanus Rathbun, Proc. U.S. Nat. Mus. vol. xxxviii, 1911, p. 577.

Material examined.—One male, three females, and two young from Gorgona Island.

Habitat.—Fine sand and small shell fragments.

Depth.—20 fathoms.

Remarks.—The material examined agrees with Milne-Edwards's description, but the lateral borders are more strongly arched than they are represented in his figure; the frontal teeth are blunter, and the inferior border of the orbit is not so pointed. Verrill states that he personally has seen no specimens agreeing well with Milne-Edwards's figure of 1879 (?). But at least the shape of the frontal teeth can be seen in a series of specimens to vary exceedingly with age. These specimens, however, are nearer *P. (Achelous) spinimanus* than *P. (Achelous) brevimanus*, the Pacific form described by Faxon, which Miss Rathbun separates as a distinct species representing *spinimanus* on the Pacific. No satisfactory critical results, however, can be obtained from such immature specimens.

Measurements (largest specimen in material, male, length 15.0 mm.; smallest, male, 8.5 mm.) :—

	mm.
Length of carapace	15.0
Breadth of carapace+lateral spines	25.75
Breadth of carapace between last antero-lateral spines	22.5
Breadth of orbit.....	6.0

Range.—From Cape Hatteras to Rio de Janeiro, Brazil; Coast of Chile.

Portunus (Achelous) brevimanus from Cocos Island, Galapagos Islands.

PORTUNUS (ACHELOUS) SPINICARPUS (Stimpson).

Achelous spinicarpus Stimpson, Bull. Mus. Comp. Zool. Harv. vol. ii, 1870, p. 148.

Neptunus spinicarpus A. Milne-Edwards, Miss. Scient. Mex. 1880, p. 221, pl. xl, fig. 1.

Portunus (Achelous) spinicarpus Rathbun, Bull. U.S. Comm. Fish. Wash. vol. xx, 1901, p. 47.

Portunus spinicarpus Hay & Shore, Bull. U.S. Bureau Fish. vol. xxxv, 1918, p. 429, pl.

Material examined.—Two males from Gorgona Island.

Habitat.—Fine sand and small shell fragments.

Depth.—20 fathoms.

Remarks.—After comparing the material obtained by S.Y. 'St. George' from the Pacific with numerous Atlantic specimens in the British Museum, the only modification observed was that the two cardiac tubercles, although

well defined in the Atlantic forms, are more precise in the specimens from the Pacific.

Measurements :—

Length of carapace	22.0
Breadth of carapace+lateral spines	43.0
Breadth of carapace without lateral spines	34.0

Range—North Carolina to Sabanillo, Colombia, West Indies. Recorded now from Gorgona Island, Pacific.

PORTUNUS (ACHELOUS) TUBERCULATUS (Stimpson).

Achelous tuberculatus Stimpson, Ann. Lye. Nat. Hist. N.Y. vol. vii, 1862, p. 223 ;
A. Milne-Edwards, Miss. Scient. Mex. pt. 5, 1880, p. 221, pl. xxxix, fig. 1.

Material examined.—One female and three males from Gorgona Island.

Habitat.—Shells, dead coral, and gravel overgrown with Polyzoa and *Lithothamnium*.

Depth.—15 fathoms.

Measurements (largest specimen in material, a female) :—

	mm.
Length of carapace	8.0
Breadth of carapace+antero-lateral teeth	16.0
Breadth of carapace between antero-lateral teeth	12.0
Breadth of fronto-orbit	3.5

Range.—Cape St. Lucas. Recorded now from Gorgona Island.

PORTUNUS (ACHELOUS) ANGUSTUS Rath.

Portunus (Achelous) angustus Rathbun, Proc. U.S. Nat. Mus. vol. xxi, 1899, p. 594,
pl. xlii, fig. 2 ; Proc. Wash. Acad. Sci. vol. iv, 1902, p. 282 ; Proc. U.S. Nat. Mus.
vol. xxxviii, 1911, p. 578 ; Boone, Zoologica, N.Y. vol. viii, no. 4, 1927, p. 181, fig.

Material examined.—One male specimen from Galapagos Islands.

Depth.—Shore.

Remarks.—The cheliped of the male shows exactly the same characters as that of the female, with the exception that on the hand there is a third exceedingly small spine. It is situated just above the articulation of the dactylus, and is in direct line with the second spine of the manus, which has its position on the superior margin, one-third of its length from the dactylus. In this specimen the inferior margin of the merus in *both* natatory feet is armed with *one* spine, the left not differing in any way from the right. The abdomen of the male is roughly triangular, seven-jointed, with the fourth and fifth segments showing a tendency to fuse ; first five segments transversely carinated.

Measurements :—

	mm.
Length of carapace	16.3
Breadth of carapace	24.0

Range.—Galapagos Islands.

Genus *CRONTUS* Stimpson.*CRONTUS RUBER* (Lamarck).

Portunus ruber Lamarck, Hist. Nat. Anim. sans. Vert. vol. v, 1918, p. 260.

Cronius ruber Rathbun, Zoologica, N.Y. vol. v, no. 14, 1924, p. 159; Boone, Zoologica, N.Y. vol. viii, no. 4, 1927, p. 182, fig. 62.

Material examined.—One male from Gorgona Island.

Habitat.—Shells, dead coral, and gravel overgrown by Polyzoa and *Lithothamnium*.

Depth.—15 fathoms.

Measurements :—

	mm.
Length of carapace	9.5
Breadth of carapace + antero-lateral spines	15.0
Breadth of carapace between last antero-lateral spines	13.5
Breadth of fronto-orbit	5.0

Range.—From South Carolina to Rio de Janeiro, Brazil; Lower California to Ecuador.

Genus *LUPELLA* Rathbun.*LUPELLA FORCEPS* (Fabricius).

Cancer forceps Fabricius, Ent. Syst. auct. et emend. vol. ii, 1793, p. 449.

Lupella forceps Rathbun, Bull. U.S. Fish Comm. vol. xx, pt. 2, 1900, p. 50.

Material examined.—Two females and five males from Gulf of Paria, Trinidad.

Depth.—3–6 fathoms.

Measurements (largest specimen examined, female, length 16.0 mm.; smallest, male, length 7.0 mm.):—

	mm.
Length of carapace	16.0
Breadth of carapace + lateral spines	41.0
Breadth of carapace without lateral spines	27.0

Range.—West Indies.

Genus *POLYBIUS* Leach.*POLYBIUS HENSLOWI* Leach.

Polybius henslowi Leach, Malacostraca Podophthalmata Britanniae, 1815, Tab. 98, figs. 1–4; Carrington & Lovell, Zoologist, Lond. vol. xl, 1881, p. 98; Sinel, J., Trans. Soc. Nat. Sci. Guernsey, 1906, p. 215; Legendre, R., Bull. Soc. Zool. Fr. T. 49, 1924, p. 364; Perez, C., t. c. p. 375.

Material examined.—Young female, body soft just after a moult. A definite locality has not been stated, but the label bears the date "17–4–24"; in all probability this specimen was collected from a locality from which it has already been reported, and, therefore, is not of particular interest in the present paper.

Measurements :—

	mm.
Length of carapace	14.0
Breadth of carapace	15.0

Range.—South coast of England ; West coasts of France and Spain.

Family XANTHIDÆ.

Genus XANTHO Leach.

XANTHO STIMPSONI (Stimpson).

Xantho denticulatus Stimpson, Ann. Lye. Nat. Hist. N.Y. vol. vii, 1862, p. 207.

Xantho stimpsoni A. Milne-Edwards, Miss. Scient. Mex. pt. 5, 1880, p. 252, pl. xlvii. fig. 2.

Material examined.—One female from Taboga Island, Bay of Panama.

Habitat.—From dead coral.

Depth.—Just below low tide mark.

Remarks.—The antero-lateral teeth in this specimen are alternately large and small ; 1st, small (Stimpson regards this tooth as belonging to the subhepatic region) ; 2nd, large ; 3rd, small ; 4th, large ; 5th and 6th, small ; 7th, large ; 8th, small ; 9th, large.

Measurements :—

	mm.
Length of carapace	6.5
Breadth of carapace	9.0
Breadth of fronto-orbit.....	6.0
Breadth of front	3.0

Range.—Cape St. Lucas. Recorded now from Taboga Island, Panama.

Genus LEPTODIUS A. Milne-Edwards.

LEPTODIUS SNODGRASSI Rathbun.

Leptodius snodgrassi Rathbun, Proc. Wash. Acad. Sci. vol. iv, no. 8, 1902, p. 279, pl. xii, figs. 7 & 8.

Material examined.—Two males and four females from Conway Bay, Indefatigable Island, Galapagos Islands.

Habitat.—Shore pools. This station includes a very productive peat bed, which extends below lowest tide levels.

Remarks.—The specimens vary considerably in the degree of areolation, some presenting a much more "withered" appearance than others.

Measurements (largest specimen examined, male) :—

	mm.
Length of carapace	8.0
Breadth of carapace	12.5
Breadth of fronto-orbit.....	7.2
Breadth of front	3.5

Range.—Galapagos Islands.

Genus *ACTÆA* de Haan.*ACTÆA DOVII* Stimpson.

Actæa dovi Stimpson, Ann. Lyc. Nat. Hist. N.Y. vol. x, 1874, p. 104; A. Milne-Edwards, Miss. Scient. Mex. pt. 5, 1880, p. 244, pl. xlv, fig. 1; Rathbun, Proc. U.S. Nat. Mus. vol. xxxviii, 1911, p. 583; Boone, Zoologica, N.Y. vol. viii, no. 4, 1927, p. 203, fig.

Material examined.—Numerous specimens from Taboga, Gorgona, Coiba, and Galapagos Islands.

Habitat.—Coral, sand, and weed.

Depth.—To 12 fathoms.

Remarks.—Young specimens about 4 mm. in length had the antero-lateral border more deeply cleft than the adults. My observations on the colour of the specimens agree with Boone's notes :—"The very young specimens of the species, about 3-5 mm. wide, have alternate red and cream-white stripes radiating from the central part of the posterior region outward to the frontal and lateral margin. In older specimens, 10 mm. or more wide, the stripes are replaced by solid orange-red coloration." The 'St. George' specimens, however, had been in spirit for some time and the bands were a dark bluish purple.

Measurements (largest specimen in material, a female) :—

	mm.
Length of carapace	10.0
Breadth of carapace	15.0
Breadth of fronto-orbit.....	4.5

Range.—Panama; San Salvador; Ecuador, Galapagos Islands.

ACTÆA SULCATA Stimpson.

Actæa sulcata Stimpson, Ann. Lyc. Nat. Hist. N.Y. vol. vii, 1862, p. 203; A. Milne-Edwards, Miss. Scient. Mex. pt. 5, 1880, p. 246.

Material examined.—One female and one male from Gorgona Island.

Remarks.—Ambulatory feet sulcated and granulated.

Measurements (female is the larger specimen) :—

	mm.
Length of carapace	5.0
Breadth of carapace	8.0
Breadth of fronto-orbit..	3.0

Range.—Cape St. Lucas. Recorded now from Gorgona Island.

Genus *GLYPTOXANTHUS* A. Milne-Edwards.*GLYPTOXANTHUS LABYRINTHICUS* (Stimpson).

Actæa labyrinthica Stimpson, Ann. Lyc. Nat. Hist. N.Y. 1862, vol. vii, p. 204.

Actæa meandricus Lockington, Proc. Calif. Acad. Sci., Sept. 1877, p. 97.

Glyptoxanthus labyrinthicus A. Milne-Edwards, Miss. Scient. Mex. pt. 5, 1880, p. 255, pl. xliii, fig. 4; Rathbun, Bull. Amer. Mus. Nat. Hist. N.Y. 1923, vol. xlviii, Article 20, p. 622.

Material examined.—One female from Gorgona Island.

Habitat.—From colonies of *Pocillopora*.

Measurements :—

	mm.
Length of carapace	32·0
Breadth of carapace	22·0

Range.—Lower California to Panama. Recorded now from Gorgona Island.

Genus PLATYPODIA Bell.

PLATYPODIA ROTUNDATA (Stimpson).

Atergalis rotundatus Stimpson, Ann. Lyc. Nat. Hist. N.Y. vol. vii, 1862, p. 202.

Platypodia rotundata Rathbun, Proc. U.S. Nat. Mus. vol. xxxviii, 1911, p. 584.

Material examined.—One much damaged female from Galapagos Island.

Habitat.—Coarse clean sand and abundant weeds. Washed from bucketful of *Dendrophyllia*.

Depth.—12 fathoms.

Remarks.—The ambulatory legs have two granulated costæ on carpus and propodite.

Measurements :—

	mm.
Length of carapace	7·0
Breadth of carapace	10·0

Range.—Cape St. Lucas, Panama. Recorded now from Galapagos Islands.

PLATYPODIA GEMMATA Rathbun.

Platypodia gemmata Rathbun, Proc. Wash. Acad. Sci. vol. iv, no. 8, 1902, p. 279,

pl. xii, figs. 5 & 6 ; Proc. U.S. Nat. Mus. vol. xxxviii, 1911, p. 584.

Material examined.—Five males and one female from Galapagos Islands ; six males and eight females from Taboga Island.

Habitat.—Coarse sand and abundant weeds, including *Rhodophyceæ* and *Lithothamnium*. Also from under floating pier.

Remarks.—None of the specimens from Taboga Island have the furry character noted by Miss Rathbun on the Galapagos specimens, but the specimens from Galapagos agree with her description in this detail also.

Measurements (largest specimen in material, a female) :—

	mm.
Length of carapace	11·0
Breadth of carapace	16·0
Breadth of fronto-orbit	4·5

Range.—Galapagos. Recorded now from Taboga Island, Bay of Panama.

Genus *XANTHIAS* Rathbun.*Key to Species of Xanthias dealt with in this Paper.*

- a. Frontal border with margin thick and swollen.
 - b. Areolated lobes of carapace strongly granulate *crosslandi*, sp. n.
 - b'. Areolated lobes of carapace smooth *insculpta* Rath.
- a'. Frontal border with margin distinct and crenulate.
 - b. Granulations on carapace confined to definite rows, merus of ambulatory legs without teeth on upper border *margaritata*, sp. n.
 - b'. Granulations on carapace not confined to definite rows, merus of ambulatory legs with upper border serrulate *serrulata*, sp. n.

XANTHIAS INSCULPTA (Stimpson).

Xanthodes insculpta Stimpson, Ann. Lyc. Nat. Hist. N.Y. vol. x, 1874, p. 105;
 Rathbun, Zoologica, N.Y. vol. v. no. 14, 1924, p. 157, fig. 38; Boone, Zoologica, N.Y.
 vol. viii, no. 4, 1927, p. 207, figs. 74 A & B.

Material examined—Nine males and two females from Galapagos Islands.

Habitat.—*Lithothamnium* nodules.

Depth.—To 4 fathoms.

Measurements (largest specimen in material, a male):—

	mm.
Length of carapace	5.0
Breadth of carapace	7.0
Breadth of fronto-orbit.....	4.3
Breadth of front	2.5

Range.—Cape St. Lucas; Galapagos Islands.

XANTHIAS SERRULATA, sp. n.

Material examined.—Four females, one male, and seven young from Gorgona Island.

Habitat.—Among colonies of *Pocillopora*.

Depth.—Below low tide mark.

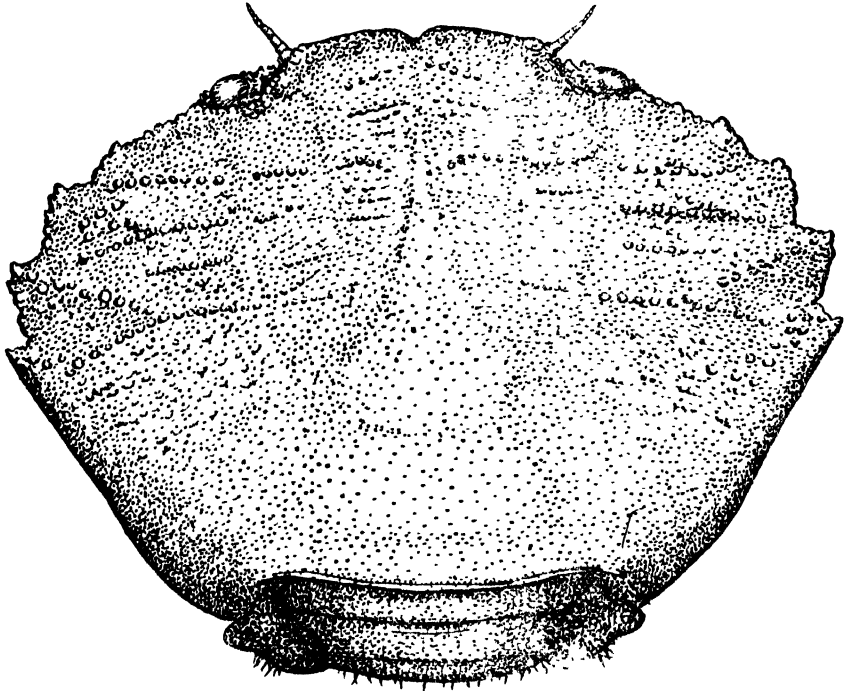
Description.—Borders of antero-lateral and frontal regions together form an arch extending downwards on each side to rather more than half the length of the carapace. The postero-lateral borders are rounded and strongly convergent; posterior borders well defined and narrow. Chelipeds not hidden by carapace from dorsal view. Fronto-orbital border more than half the greatest width of the carapace. Anterior third of carapace strongly areolated; areas defined posteriorly as far as the cardiac region. The entire surface of the carapace, excluding the cardiac region, is studded with granules which become more and more pronounced laterally and anteriorly, where they are bead-like and form definite transverse lines or ripples, some of which are more accentuated than others.

Describing the general appearance given by these to the surface, MacGilchrist, writing on *X. cumatodes* says, "these rows occupy the tops of successive small ridges which look like wavelets or ripples moving in a forward direction."

Front divided by a V-shaped emargination into two straight lobes. From the external teeth of the frontal margin there runs inwards, parallel with the margin, a row of beaded granules, giving the double-edge appearance described by MacGilchrist for *X. cumatodes*, and figured by Milne-Edwards and Bouvier for *X. granosus*. On the frontal lobes numerous granules are scattered indiscriminately: posterior boundary of each lobe defined by a groove.

The gastric region is divided into three sub-regions—two protogastric regions, and a median one formed by the fusion of meso-, meta-, and urogastric areas. Each protogastric region is divided by a slight longitudinal groove which does

TEXT FIG. 6.

*Xanthus serrulata*, sp. n., $\times 12$.

not extend to the hinder border of the region; the subdivisions are supplied anteriorly with a concise row of granules, behind which, at close intervals, a series of such rows occur growing gradually more and more faint. Hepatic region more or less depressed, with an oblique row of four, five, or six small bead-like tubercles running back from the external angle of the orbit to a point just internal to the first antero-lateral tooth. From the dorsal view, two small subhepatic tubercles are seen.

There are four antero-lateral teeth, the surface and summits of which are roughly granular; first and last are the smallest, and the last usually the smaller of the two. Branchial region well supplied with granulated ridges. At its

anterior limit it has an oblique row of granules stretching across from the cervical groove almost to the second antero-lateral tooth. Posterior to this are other transverse ridges, the most prominent being the next one of the series and one at a level just anterior to the last antero-lateral tooth. Some quite distinct, but much smaller, ridges run between the second and third, and from the summits of the third and fourth antero-lateral teeth, but the entire surface of the branchial region is lined and puckered by subsidiary wavelets. Cardiac region punctate, and posterior border closely granulate.

Orbits neat, groove indistinct. Margin of orbit shows same double-edge effect on front as far as position of first fissure. Inferior margin with denticulated lobes at outer and inner angles. A "dog's ear" flap projects from the eye-stalk on the dorsal surface of the cornea as in *X. cumatodes*; the projection is granular and not provided with a tuft of setæ. The transverse row of granules on the front of the eye-stalk just internal to the cornea are all equal and dentiform.

Basal antennal joint short, just reaches process from front, flagellum not as long as greatest width of orbit. Chelipeds unequal. Merus punctate; carpus tubercular, and with setæ sparsely covering the surface, a deep transverse groove, tooth on superior distal border and smaller one behind at upper border of inner surface. Manus punctate, inner surface with suggestion of granulation towards proximal end. Merus with outer surface tubercular, more granular near inferior border; three longitudinal furrows, a deep one on superior border, another deep one close to it on outer surface, and a third less distinct one also on the outer surface.

Fingers dark brown; upper finger with two ridges, granular at proximal extremity and with one large tooth and two small ones; lower finger with several small teeth, prominent carina extends just beyond coloured portion. Ambulatory legs:—merus serrated, carpus of 1st, 2nd, and 3rd legs with single row of granules, carpus of 5th smooth; carpus, propodus, and dactylus of 2nd, 3rd, and 4th setiferous, setæ restricted to borders on last leg.

Remarks.—This species is close to *X. melanodactylus* A. Milne-Edwards, *X. granosus* Milne-Edwards & Bouvier, and *X. cumatoides* MacGilchrist.

From *X. melanodactylus* it may be distinguished by the following characters:—

- (a) It is not only on the gastric region that the granules are arranged in transverse lines.
- (b) Orbits granular.
- (c) Fingers black, but do not bear white denticles.
- (d) Ambulatory legs not "smooth and sleek," last article not devoid of hairs.

From *X. granosus* it may be distinguished by the following characters:—

- (a) Front less sinuous, less projecting.
- (b) Transverse rows of granules on carapace not as oblique as those represented on *X. granosus*.
- (c) Manus of cheliped with three longitudinal grooves, not two.
- (d) Propodus of last pair of ambulatory legs relatively longer.

From *X. cumatodes*, it may be distinguished by the following characters :—

- (a) Branchio-hepatic regions not so clearly divided into the four areas—one marginal, two dorsal, and an internal triangular one.
- (b) Dorsal view allows two small hepatic tubercles to be seen between the first tooth and external orbital angle.
- (c) The uppermost granule on front of eye-stalks not markedly different from the rest.
- (d) Granules on carpus of cheliped sharper.
- (e) No hump is present in the middle of the anterior margin of the carpal joint.

Measurements (female) : —

	mm.
Length of carapace	6.0
Breadth of carapace	8.5
Breadth of fronto-orbit.....	4.5
Breadth of front	2.8

XANTHIAS MARGARITATA, **sp. n.**

Material examined.—One female from Balboa, Panama

Habitat.—Rocks and rock-pools.

Depth.—At low tide mark.

Description.—General shape of carapace broadly oval, frontal and antero-lateral borders together forming a wide arch, postero-lateral borders convergent. Fronto-orbital border not much more than half the width of the carapace. Surface of carapace punctate and shining, anterior two-thirds areolated and lobulate. Two frontal lobes with transverse row of granules anteriorly : directly posterior to these are two smaller protogastric lobes. From the depressions between the second and third normal antero-lateral teeth, four transverse rows of granules extend across the carapace, one on each epibranchial region, and one on each protogastric region medianly. Two other rows of well developed granules occur on the mesobranchial areas, and another short row behind this. Just above the junction of the posterior and postero-lateral borders is a small nodule. The remainder of the carapace, apart from slightly marked bunches of granules, is smooth and glabrous.

Front between one-third and one-fourth width of carapace, moderately produced, with small median notch ; borders granulate and slightly sinuous, lateral angles strongly marked. Superior margin of orbit pronounced, broad tooth at internal angle, the two fissures above distinct, strong tooth at outer angle ; inferior border granulate and bulging, with wide V-shaped notches below outer angle and tooth at inner angle.

Antero-lateral margin with four teeth, excluding orbital tooth. Orbital tooth much smaller than succeeding teeth : 1st antero-lateral tooth broad, with thickened edge ; 2nd tooth double, small subsidiary tooth anteriorly, remainder of tooth resembling 1st in shape ; 3rd tooth largest, concave anterior

border armed with spiny denticles, beaded ridge runs from apex inwards towards branchial region ; 4th tooth smaller and more acute.

Basal antennal joint with inner border produced to meet process from front and outer produced into orbital hiatus, does not exclude flagellum ; flagellum one and a half times width of orbit.

Subhepatic region with granular ridge running transversely towards first antero-lateral tooth, broken in the middle by depression.

Chelipeds nodular, transverse carpal groove anteriorly, nodules arranged more or less definitely in three rows. Manus of large cheliped with two rows of nodules on superior border and third less distinct row on outer surface of hand. Fingers grooved, light in colour, provided with well-developed teeth ; dactylus with strong basal tooth. Ridges on manus of small cheliped more marked, general surface less smooth.

Ambulatory legs, with merus smooth but with a few long hairs, minute spines on upper border ; carpus with three longitudinal rows of granules ; propodus and dactylus hairy.

Measurements :—

	mm.
Length of carapace	7.5
Breadth of carapace	11.0
Breadth of fronto-orbit.	6.0
Breadth of front	3.0

XANTHIAS CROSSLANDI, sp. n.

Material examined.—Three females from Tagus Cove, Galapagos Islands.

Habitat.—Weed, broken shells, etc.

Depth.—12 fathoms.

Description.—Carapace broadly oval, surface strongly areolated in anterior two-thirds, granular, the granules becoming exceedingly pronounced on the branchial areas. Front divided by small median fissure into two broad straight lobes which are not produced laterally, although the lateral granules may be stronger than others on margin of front.

Frontal lobes evenly granulate. Gastric region divided into protogastric areas and a single median area. The protogastric area is further subdivided by a longitudinal furrow, which does not quite reach its posterior boundary, and by a short furrow anteriorly cutting off two lobules directly posterior to the frontal lobes. Hepatic region coarsely granular. Mesobranchial region is delimited anteriorly by a furrow running inwards from the base of second antero-lateral tooth, and posteriorly by a groove from between the 3rd and 4th antero-lateral teeth. In the largest specimen examined, the most conspicuous granules are those which run inwards from the base of the last antero-lateral tooth, at the anterior boundary of the metabranchial region ; in the smaller specimens the most conspicuous are those which occur on the epibranchial region and tend to form two short transverse lines. Mesobranchial area with granules grouped into bunches.

Antero-lateral border with four tuberculated teeth—1st depressed, 2nd larger than 1st, blunter than 3rd and 4th ; margin between the teeth with numerous small tubercles.

Orbits with two distinct fissures above ; superior margin with beaded granules, inferior with spiny granules and lobe at inner angle. Subhepatic region deeply grooved, with transverse row of granules from 1st antero-lateral tooth. Basal antennal joint and eye-stalk also granular. Merus of 3rd maxilliped with anterior border, slightly produced laterally, and with marked depression running from notch on anterior border at base of palp posteriorly in oblique direction ; inner border also slightly produced. Chelipeds tubercular, merus with two teeth on upper border, carpus with large tubercle at angle of antero-internal border, and sharp tooth internal to it ; largest tubercles on upper portion ; tubercles on manus of large cheliped arranged more or less in rows ; these rows are more definite and tubercles sharper on small cheliped. Fingers grooved and provided with strong teeth, two equally well developed teeth at base of dactylus in large cheliped ; colour very light brown or horn colour, not extending at all on to the hand.

Ambulatory legs with spiny granules, not confined to upper margin in the carpus and propodus. Numerous hairs occur on all the joints, particularly propodus and dactylus.

Remarks.—Resembles *X. granulimanus* of Stimpson, but differs from it in the following respects :—

- (a) Granules especially conspicuous not only on hepatic, but also on branchial regions.
- (b) Antero-lateral teeth not equal and triangular.
- (c) Granulated ridge extends inwards from the last tooth, broken ridge extends from the penultimate tooth.
- (d) Basal joint of external antenna meets the front.

Measurements (largest specimen in material) :—

	mm.
Length of carapace	7.5
Breadth of carapace	10.5
Breadth of fronto-orbit.....	7.0
Breadth of front	3.8

Genus *PANOPEUS* H. Milne-Edwards.

PANOPEUS BERMUDENSIS Benedict & Rathbun.

Panopeus bermudensis Benedict & Rathbun, Proc. U.S. Nat. Mus. vol. xiv, 1891, p. 376, pl. xx, fig. 2, pl. xxiv, figs. 14–15 ; Rathbun, Proc. U.S. Nat. Mus. vol. xxxviii, 1911, p. 542, fig.

Material examined.—Numerous specimens from Colon ; Balboa ; Tobago and Coiba Islands, Bay of Panama.

Habitat.—Piles and floats, also rocks and rock pools.

Depth.—Low tide mark.

Remarks.—The specimens from Colon approach nearer to Verrill's var. *sculptus* than did the Pacific forms, but none of them are that variety.

Measurements (largest specimen in material) :—

	mm.
Length of carapace	5.0
Breadth of carapace	7.0
Breadth of fronto-orbit.....	4.9
Breadth of front	3.0

PANOPEUS SERRATUS de Saussure.

Panopeus serratus de Saussure, Rev. et Mag. de Zool. ser. 2, vol. ix, 1857, p. 502 ; Benedict & Rathbun, Proc. U.S. Nat. Mus. vol. xiv, 1891, p. 371, pl. xxiv, figs. 3 & 4.

Material examined.—Two young males from Taboga Island, Bay of Panama.

Habitat.—Floating stage at end of pier.

Measurements (largest specimen) :—

	mm.
Length of carapace	5.0
Breadth of carapace	7.0
Breadth of fronto-orbit.....	4.8
Breadth of front	2.5

Range.—Florida ; West Indies. Recorded now from Taboga Island, Bay of Panama.

PANOPEUS BRADLEYI Smith (?).

Panopeus bradleyi Smith, Proc. Boston Soc. Nat. Hist. vol. xii, 1869, p. 281 ; Rathbun, Proc. U.S. Nat. Mus. vol. xxxviii, 1911, p. 584.

Material examined.—Four mutilated young specimens from Galapagos Islands.

Habitat.—Sand and weed.

Remarks.—These young forms are doubtfully referred to this species.

Measurements (largest specimen in material, a male) :—

	mm.
Length of carapace	5.0
Breadth of carapace	7.0
Breadth of fronto-orbit.....	4.8
Breadth of front	2.5

Range.—Panama. Recorded now, with some uncertainty as to species, from Galapagos Islands.

PANOPEUS LÆVIS Dana (?).

Panopeus laevis Dana, U.S. Exploring Expedition, Crust. pt. 1, 1852, p. 180, pl. viii, figs. 13 a, b, & c.

? *Panopeus laevis* Miers, Report ' Challenger ' Expedition, vol. xvii, 1886, p. 129.

Material examined.—One damaged male from Taboga Island, Bay of Panama.

Habitat.—Under floating stage at end of pier.

Measurements :—

	mm.
Length of carapace	6.5
Breadth of carapace	9.0
Breadth of fronto-orbit.....	6.0
Breadth of front	3.0

Range.—Dana's specimen came from an unknown locality. Stimpson refers it to West Coast of America and Miers to Brazil.

Genus *HEXAPANOPEUS* Rathbun.*HEXAPANOPEUS SETIPALPUS*, sp. n.

Material examined.—Ten females and three males from Taboga Island, Bay of Panama.

Habitat.—Corals.

Depth.—To 5 fathoms.

Description.—Carapace hexagonal, regions markedly areolate and minutely granulated. Front much produced, divided medianly by a V-shaped fissure, margin oblique, rounded laterally and separated by a deep notch from the margin of the orbit.

Antero-lateral border thin, a deeper sinus between orbital tooth and first antero-lateral tooth in adult than in young, teeth resembling those of *H. angustifrons*. third tooth most pronounced and acute, the fourth least produced and post-lateral in position. Teeth separated from each other by deep grooves.

Orbit with two fissures above, margin between the fissures rounded and produced; inner border continues the downward curve of the front, making a very marked angle with the rest of the superior border. Inferior border with gaping fissure under outer angle, straight and scarcely produced at all at inner angle, entirely devoid of teeth. Very prominent tooth-tubercle on summit of eye-stalk. Basal antennal joint short and broad, inner angle occupying orbital hiatus; subhepatic region without tooth, smooth.

External maxilliped with inner anterior border of ischium produced, throwing merus outward, merus with external distal and internal proximal angles produced; palp greatly developed, extending beyond the front, with long setæ curving forwards.

Abdomen of males with five joints, third, fourth, and fifth segments fused, outline of fused portion deeply concave from the middle of the third segment: third segment produced laterally, but not as wide as first segment; second segment narrow, leaving seventh sternal plate broadly exposed.

Merus of cheliped not toothed, a blunt tubercle at articulation with carpus, carpal groove present but indistinct, carpus with tooth on superior border and ill-defined tubercles on outer surface. Hand smooth and glabrous, dactylus without basal tooth, bent strongly downwards; finger of propodus with two small teeth near its articulation with the dactylus; fingers widely gaping and overlapping.

Ambulatory legs slender, dactylus long and hairy, carpus of two last legs broad, with hairs regularly arranged on inferior margin.

Colour of specimens in alcohol, cream : fingers black to horn-colour, lighter at tip, and colour extending a short distance back on the manus.

Remarks.—Close to *H. angustifrons* (Ben. & Rath.), but differs from it in the following respects :—

- (a) Basal tooth on dactylus is wanting.
- (b) Colour of fingers extends back on to the hand.
- (c) Orbital tooth and first antero-lateral tooth coalesced, sinus *not* shallower in adult than in the young form.
- (d) Inner lower angle of orbit *not* pointed or much produced.
- (e) Character of third maxillipeds:
- (f) Third segment of abdomen of male *not* as wide as the first, sides produced, not rounded.

Measurements (largest specimen in material) :—

	mm.
Length of carapace	5.5
Breadth of carapace	7.5
Breadth of fronto-orbit	4.9
Breadth of front	3.0

Range of Genus.—From Massachusetts to Brazil, West Indies. Recorded now from the Pacific area.

Genus PILUMNUS Leach.

PILUMNUS FRAGOSUS A. Milne-Edwards.

Pilumnus fragosus A. Milne-Edwards, Miss. Scient. Mex. pt. 5, 1880, p. 296, pl. 11, fig. 1.

Pilumnus fragosus var., Miers, Report 'Challenger' Expedition, vol. xvii, Brachyura, 1886, p. 153.

Material examined.—One female and three young from Taboga Island, Bay of Panama.

Habitat.—From floats of the stage at end of pier.

Remarks.—These specimens approach the condition of Miers's variety collected at Bahia, but these distinctions are almost certainly due to difference in age. The younger forms from Taboga are provided with more numerous, longer hairs, but are less generally pubescent than the old form.

Measurements :—

	mm.
Length of carapace	7.5
Breadth of carapace	9.5

Range.—St. Thomas Island ; Bahia. Recorded now from the Pacific, from Taboga Island, Bay of Panama.

PILUMNUS SPINULIFER Rathbun.

Pilumnus spinulifer Rathbun, Proc. U.S. Nat. Mus. vol. xxi, no. 1162, 1899, p. 585, pl. xlii, figs. 6-8, vol. xxxviii, no. 1766, p. 585; Boone, Zoologica, N.Y. vol. viii, no. 4, 1927, p. 217, fig. 79.

Material examined.—One male and two females from Galapagos Islands.

Habitat.—Among weeds and broken shells.

Depth.—12 fathoms.

Measurements (largest specimen in material, a female) :—

	mm.
Length of carapace	10.0
Breadth of carapace	7.0

Range.—Galapagos Islands, Cape St. Lucas.

PILUMNUS CROSSLANDI, sp. n.

Material examined.—One female and three young males from Galapagos Islands.

Habitat.—Coarse clean sand and abundant weeds.

Depth.—12 fathoms.

Description.—Carapace covered, at least in anterior two-thirds, with stiff yellow hairs, among which numerous long hairs are scattered promiscuously, except on the frontal region, where they form a definite fringe across: posterior portion of carapace with a few long hairs, but almost entirely devoid of pubescence. Legs and chelipeds thickly covered with stiff setæ and hairs. Shape of carapace somewhat globose, not much broader than long, strongly deflexed anteriorly: regions well defined, surface when hairs are removed granular; there is a row of four small tubercles across the frontal lobes, and numerous small tubercles occur on the gastric, hepatic, and branchial regions—these are best developed on the hepatic and branchial areas; posterior portion of the carapace punctate.

Front about one-third width of carapace; slightly crenate and divided into two lobes by a long, narrow, V-shaped fissure; margins of lobes with spinules. Antero-lateral border shorter than postero-lateral border; with four spines, excluding orbital spine; first spine much smaller than orbital spine or the other three spines of the antero-lateral border, and placed at a lower level than these, yet not actually on subhepatic region.

Orbital margins closely beset with stiff hairs; superior margin with spine at inner and outer angle, spinules on its border, fissures indistinct; inferior border with similar spines and spinules.

Basal antennal joint long, meets the front at its inner angle. Subhepatic region smooth.

Merus of external maxillipeds slightly produced at outer angle.

Sternum and abdomen of male smooth, but provided with sparse tufts of hair.

Chelipeds very unequal; merus with two broad teeth on upper margin; carpus with spine at inner angle, and usually two or three subsidiary spines:

a row of spines along distal border and several others on outer surface ; manus of large cheliped with sharp spinulous granules arranged in longitudinal rows on upper half, which become more rounded and arranged with less precision on lower half ; claws bluntly denticulated, granulated at base in large cheliped, dactylus of large cheliped with small basal tooth. Carpus and manus of smaller cheliped with spines, less numerous and somewhat less definitely arranged than granules of larger hand, claws armed at base with spinules. Ambulatory legs with merus very lightly fringed with hairs, all the other joints thickly provided with hairs, particularly on upper borders, carpus with slight longitudinal groove.

Colour of specimens preserved in spirit is light yellow-brown, spines dark brown, claws black at base, light at tips.

Remarks.—Seems to be nearer *P. africanus* A. Milne-Edwards than any of the American species.

Measurements (female) :—

	mm.
Length of carapace	11.5
Breadth of carapace	14.5
Breadth of fronto-orbit.	10.0
Breadth of front	5.0

Genus HETERACTÆA Lockington.

HETERACTÆA LUNATA (Milne-Edwards & Lucas).

Pilumnus lunatus Milne-Edwards & Lucas, 'Voyage dans l'Amérique méridionale d'Orbigny,' Crustacés, 1844, p. 20, pl. ix, fig. 2 ; Gay, *Historia de Chile*, 1849, t. 3, p. 145 ; Stimpson, *Ann. Lyc. Nat. Hist. N.Y.* vol. vii, 1862, p. 216 ; Streets & Kingsley, *Bull. Essex Inst.* vol. ix, p. 106.

Heteractæa lunata A. Milne-Edwards, *Miss. Scient. Mex.* pt. 5, 1880, p. 301, pl. lii, figs. 2 & 3 ; Rathbun, *Mem. Mus. Comp. Zool. Cambridge, Mass.*, Coll. xxxv, 1907, p. 71 ; *Bull. U.S. Nat. Mus.* No. 103, 1918, p. 171, figs.

Material examined.—Seventeen specimens from Taboga Island, Bay of Panama ; more than half the number young.

Habitat.—From coral and from under floating stage at end of pier.

Depth.—Just below low tide mark.

Measurements (largest specimen in material, male) :—

	mm.
Length of carapace	8.0
Breadth of carapace	13.0
Breadth of fronto-orbit.	10.0
Breadth of front	5.0

Range.—From San Diego, California, to Chile. Fossil from Atlantic side of Costa Rica, Pleistocene.

Genus PSEUDOZIUS Dana.

PSEUDOZIUS CAYSTRUS (Adams & White).

Panopeus caystrus Adams & White, Zoology of the Voyage H.M.S. 'Samarang,' Crustacea, p. 42, pl. ix, fig. 2.

Pseudozium planus Dana, Proc. Acad. Nat. Sci. Philad. 1852, p. 81; U.S. Exploring Expedition, Crustacea, 1852, pt. 1, p. 233, pl. xiii, figs. 6 a-h; Richters, Beiträge zur Meeresfauna der Insel Mauritius und der Seychellen, 1880 Decapoda, p. 148; Stimpson, Smithsonian Misc. Coll. vol. xlix, 1907, p. 61.

Pseudozium caystrus Miers, 'Challenger' Report, no. 17, 1886, Brachyura, p. 142; Ortmann, Denkschr. med.-naturw. Ges. Jena, vol. viii, 1894, p. 49; De Man, Zool. Jahrb. Jena Syst. vol. viii, 1895, p. 525; Whitlegge, Mem. Aust. Mus. Sydney, vol. iii, 1897, p. 136; Alcock, J. Asiatic Soc. Beng. vol. lxxvii, pt. 2, no. 1, 1898, p. 181; Borradaile, Fauna & Geog. Maldives & Laccadive Archipelagoes, vol. i, pt. 3, 1902, p. 241; Rathbun, Bull. U.S. Fish Commission, vol. xxiii, pt. 3, 1906, p. 861.

Material examined.—Two females from Taboga Island, Bay of Panama. One male from Colon.

Habitat.—From under floating stage at end of pier, Taboga Island. On rotten wood from a wreck, Colon.

Remarks.—From Dana's description, the specimens from Taboga Island differ in that the hairs are *not* "few on the tarsus, mostly confined to lower side penultimate joint"; on the contrary, they are profuse on the upper side, except in the last leg, where a row of short hairs occurs on the penultimate joint. The relative measurements given by Dana are length : breadth 1 : 1.64, and those of the specimen from Taboga are 1 : 1.4; from Dana's figure the breadth is greater than that of Adams and White's specimen; this, however, may vary considerably, as in *P. dispar* (Calman, Trans. Linn. Soc. London, vol. viii, p. 14). In Alcock's diagnosis of the genus *Pseudozium* he describes the flagellum of the second antenna as "hardly as long as major diameter of the orbit," but the flagellum in these specimens, from both the Pacific and Atlantic sides of the Isthmus, is distinctly longer than the major diameter of the orbit.

The Atlantic specimen has the antero-lateral border more produced than the Pacific forms, but that is the only respect in which they vary at all.

Measurements (largest specimen in material, a female) :—

	mm.
Length of carapace	6.0
Breadth of carapace	8.5
Breadth of fronto-orbit	5.2
Breadth of front	2.5

Range.—Philippine Islands; Indo-Pacific; Hawaiian Islands; Mauritius. Recorded now from Panama (both sides).

Genus TRAPEZIA Latreille.

TRAPEZIA CYMODOCE var. FERRUGINEA (Latreille).

Trapezia ferruginea Latreille, Encycl. Méth. Ent. vol. x. 1825, p. 695.

Trapezia cymodoce ferruginea Rathbun, Proc. U.S. Nat. Mus. vol. xxxviii, 1911, p. 586.

Material examined.—Numerous specimens from Gorgona, Taboga, and Coiba Islands. One mutilated specimen from Colon.

Habitat.—From corals.

Depth.—Below low tide mark.

Remarks.—The colour varies from orange to ferruginous. Variation occurs in the comparative development of the frontal teeth and lateral spines. No specimen, except perhaps that from Colon, can be regarded as true to the *cymodoce* type, and from the variations observed throughout the series it would seem highly probable that Miss Rathbun was right in uniting the species.

Measurements (average-sized specimen of series examined) :—

	mm.
Length of carapace	13·5
Breadth of carapace	16·0
Breadth of fronto-orbit.....	13·0
Breadth of front	8·0

Range.—Indo-Pacific region ; Mexico ; Bay of Panama ; Galapagos Islands. Recorded now from Colon.

Genus ERIPHIA Latreille.

ERIPHIA GONAGRA (Fabricius).

Cancer gonagra Fabricius, Species Insectorum, 1781, p. 505.

Eriphia gonagra H. Milne-Edwards, Hist. Nat. des Crust. t. 1, 1834, p. 426, pl. xvi, figs. 16 & 17 ; Rathbun, Bull. U.S. Fish Comm. vol. xx, 1900, p. 42.

Material examined.—One young male from Limon Bay, Colon.

Habitat.—Coral-flat.

Remarks.—The young specimen has the tubercles and granular ridges on the carapace less well developed than the adult ; in particular, the rows of tubercles parallel to the antero-lateral margin is much less distinct.

Measurements :—

	mm.
Length of carapace	7·5
Breadth of carapace	10·0
Breadth of carapace+lateral teeth.....	10·7
Breadth of fronto-orbit.....	9·0
Breadth of front	5·0

Range.—Florida Keys to Brazil, West Indies.

ERIPHIA GRANULOSA A. Milne-Edwards.

Eriphia granulosa A. Milne-Edwards, Miss. Scient. Mex. pt. 5, 1880, p. 339, pl. lvi, fig. 2 ; Rathbun, Zoologica, N.Y. vol. v, no. 4, 1924, p. 158 ; Boone, Zoologica, N.Y. vol. vii, no. 4, 1927, p. 234.

Material examined.—Two females from Conway Bay, Indefatigable Island, Galapagos Island.

Habitat.—Shore pools, peat bed.

Remarks.—A transverse row of hairs present on the frontal region directly

posterior to the two median frontal lobes ; scattered tufts of hairs occur also on the anterior portion of the carapace. The fifth tooth of the antero-lateral margin, not counting the orbital tooth, very much reduced.

Measurements (larger specimen) :—

	mm.
Length of carapace	8.0
Breadth of carapace	11.5
Breadth of fronto-orbit	6.0

Range.—Chile , Galapagos Islands.

Genus MELIA Latreille.

MELIA TESSELATA (Latreille).

Melia tessellata Latreille, Encycl. Méth. 1828, p. 705, pl. cccv, fig. 2 ; Dana, U.S. Exploring Expedition, Crust. 1852, 1, p. 242, pl. xiv, fig. 1 ; Borradaile, Proc. Zool. Soc. London, 1900, p. 580 ; id, Fauna & Geog. Maldives & Laccadive Archipelagoes, vol. 1, pt. 3, 1902, p. 250, fig. 49 ; Duerden, Proc. Zool. Soc. London, 1905, p. 497.

Material examined.—One female from Marquesas Island.

Habitat.—Corals.

Remarks.—This specimen of *Melia tessellata* collected by Dr. Crossland is bearing *Bunodeopsis* in its claws. In this instance the Actinian has wrapped itself so completely around the claw that it would not be possible for the crab to release it. As a rule, the *Sagartia* or *Bunodeopsis* is carried between the fingers of the claws, and can be discarded by the crab at will.

Measurements :—

	mm.
Length of carapace	7.2
Breadth of carapace	9.0
Breadth between orbits	3.5

Range.—Indo-Pacific ; Hawaiian Islands ; Mauritius ; Madagascar.
Recorded now from Marquesas Island.

Genus DOMECLIA Eydoux & Souleyet.

DOMECLIA HISPIDA Eydoux & Souleyet.

Domeclia hispida Eydoux & Souleyet, Voyage ' Bonite,' Zool. vol. 1, 1852, p. 235, pl. ii, figs. 5–10 ; Dana, U.S. Exploring Expedition, Crustacea, 1852, pt. 1, p. 251 ; Lucas, in Hombroton & Jacquinot, Voyage au Pôle Sud, 1853, p. 50, pl. iv, figs. 3–7 ; Stimpson, Bull. Mus. Comp. Zool. Harvard, vol. ii, 1870, no. 2, p. 145 ; A. Milne-Edwards, Nouv. Arch. Mus. Hist. nat. Paris, vol. ix, 1873, p. 263 ; Miss. Scient. Mex. pt. 5, 1880, p. 345, pl. lviii, fig. 2 ; De Man, Arch. Naturgesch. Berlin, vol. liii, Heft 1, 1887, p. 326 ; Ortman, Zool. Jahrb. Jena Syst. vol. vii, 1893, p. 478 ; Stimpson, Ann. Lyc. Nat. Hist. N.Y. vol. vii, 1862, p. 218 ; Alcock, J. Asiat. Soc. Beng. vol. lxvii, pt. 2, no. 1, 1898, p. 230 ; Rathbun, Ann. Inst. Jamaica, vol. i, 1897, p. 22 ; Bull. U.S. Fish Comm. vol. xx, pt. 2, 1901, p. 43 ; Mem. Mus. Comp. Zool. Cambridge, Mass., Coll. xxv, 1907, p. 60.

? *Neleus acanthoplorus* Desbonne & Schramm, Crust. Guadeloupe, 1867, p. 35.

Pilumnus melanacanthus Kingsley, Proc. Boston Soc. Nat. Hist. vol. xx, 1879, p. 156.

Material examined.—Numerous specimens from Gorgona Island.

Habitat.—Among corals.

Depth.—Below low tide mark.

Remarks.—Superior margin of the buccal cavity is strongly spinulate rather than finely denticulate.

Measurements (largest specimen in material, a female) :—

	mm.
Length of carapace	12.0
Breadth of carapace	14.0
Breadth of fronto-orbit	11.0
Breadth of front	7.5

Range.—Indian Ocean and Indo-Pacific ; Australia ; East and West coasts of America ; West Indies ; Cape Verde Islands ; West and South Africa.

Family POTAMONIDÆ.

Genus PSEUDOTHELPHUSA de Saussure.

? PSEUDOTHELPHUSA BOUVIERI Rathbun.

Pseudothelphusa bouvieri Rathbun, Proc. U.S. Nat. Mus. vol. xxi, 1899, p. 518, figs. 9a & b ; Nouv. Arch. Mus. Hist. nat. Paris. ser. 4, tom. vi, 1904, p. 289, pl. xiii, fig. 5.

Material examined.—Two males from Gorgona Island.

Habitat.—Collected by Miss Cheesman at some distance up a rapid stream high above sea-level.

Remarks.—The inferior external angles of the orbit not so marked as those figured by Miss Rathbun ; well marked outer orbital notch is not present in the specimens collected by Miss Cheesman. Carpus of chelipeds with small accessory tubercular spines.

Differs from *P. chilensis* in the straighter cervical sutures, which form an obtuse angle if produced, and not a right angle as in *P. chilensis* ; also the posterior margin is more indented in this species than in *P. chilensis*.

Measurements :—

	mm.
Length of carapace	49.0
Breadth of carapace	77.0
Breadth of fronto-orbit	38.0
Breadth of inferior border of front	16.0

Range.—Santa Fé de Bogota, Colombia.

Family PINNOTHERIDÆ.

Genus PINNIXA White.

PINNIXA TRANSVERSALIS (Milne-Edwards & Lucas).

Pinnotheres transversalis Milne-Edwards & Lucas in d'Orbigny's Voy. Amér. Mérid. vol. vi, pt. 1, 1843, p. 23 ; Atlas, vol. ix, 1847, pl. x, figs. 3-3 e.

Pinnixa transversalis Rathbun, Bull. U.S. Nat. Mus. No. 97, 1917, p. 131, pl. xxix, figs. 1-3.

Material examined.—One female and one male from Coiba Island.

Habitat.—Embedded in sand at low water mark, among fine sea-grass and dead coral.

Measurements (the larger specimen is a female) :—

	mm.
Length of carapace	4.5
Breadth of carapace	10.0
Breadth of fronto-orbit.....	3.0

Range.—Panama to Punta Arenas, Patagonia.

Family GRAPSIDÆ.

Genus PACHYGRAPSUS Randall.

PACHYGRAPSUS TRANSVERSUS (Gibbes).

Grapsus transversus Gibbes, Proc. Amer. Assoc. Adv. Sci. vol. iii, 1850, p. 181.

Pachygrapsus transversus Rathbun, Bull. U.S. Nat. Mus. No. 97, 1917, p. 245, pl. lxiv. figs. 2-3.

Material examined.—One female and four young from Galapagos Islands ; one male, one female, and seven young collected by Miss Cheesman in Gorgona Island.

Habitat.—The specimens from Galapagos were taken from soft cavernous tuff-rock, 2 feet above low tide mark ; rock encrusted with Polyzoa and Sponges. The specimens from Gorgona were collected from a fallen tree, Miss Cheesman notes that " these crabs inhabit the burrows of two species of beetle larvæ, *which are still there*, though apparently exposed to wetting by sea water at high spring tides. The tree appears to have been in its present position a long time."

Measurements (largest specimen in material, a female) :—

	mm.
Length of carapace	11.5
Breadth of carapace	15.0
Breadth of fronto-orbit.....	13.5
Breadth of front	8.0

Range.—California to Peru ; Galapagos Islands ; Florida to Uruguay ; Bermudas ; West Indies ; West Africa and Oriental region.

Genus PTYCHOGNATHUS Stimpson.

PTYCHOGNATHUS CRASSIMANUS, sp. n.

Material examined.—One male from Marquesas Islands.

Habitat.—Fresh-water pond.

Description.—Carapace broader than long, thin, smooth, and slightly arched from before backwards ; regions hardly indicated, but H-shaped mark in the middle quite distinct. Front prominent, faintly sinuous. Antero-lateral margin with two teeth, not counting the outer orbital tooth, first tooth larger than the second, but neither projecting from the line of the margin.

Upper margin of orbit sinuous ; lower margin straight, serrate, forming an angle with the outer orbital tooth. Anterior border of buccal cavity three-lobed, with milled edge.

Chelipeds equal, glabrous ; carpus with denticle at inner angle ; hand swollen, fingers gaping ; claws hollowed at tip, with horny edge.

Merus of first, second, and third ambulatory legs armed with a tooth on superior border distally ; carpus with short felting of hairs on superior border ; propodus and dactylus with hairs on both superior and inferior borders.

Propodus of fourth leg broader than merus ; dactylus reduced to half the length of that of the third leg.

Remarks.—Close to *P. polleni* de Man and *P. easteranus* Rathbun. It differs from Miss Rathbun's species in general appearance and by having a sharper and more clear-cut edge to the lateral and frontal borders.

Particularly it is different in :—

- (a) Width of fronto-orbit is much more than seven-eighths that of the carapace.
- (b) Outer maxilliped has merus expanded laterally more obviously than in *P. polleni*, but less than in *P. easteranus*.
- (c) Chelipeds not granular at all. Hand very much inflated ; immovable finger with only faint indication of longitudinal groove.
- (d) Merus-joint of ambulatory legs with subterminal spine, except in last pair.

Measurements :—

	mm.
Length of carapace	11.5
Breadth of carapace	13.0
Breadth of fronto-orbit	12.5
Breadth of front	5.5
Breadth at posterior border	11.5
Breadth of ischium, 3rd maxilliped	1.5

Range of Genus.—Islands of the Indo-Pacific.

Genus *SESARMA* Say.

Subgenus *HOLOMETOPUS* H. Milne-Edwards.

SESARMA (*HOLOMETOPUS*) *RICORDI* H. Milne-Edwards.

Sesarma ricordi H. Milne-Edwards, Ann. Sci. Nat. Paris, Zool. ser. 3, vol. xx, 1853, p. 183.

Sesarma (*Holometopus*) *ricordi* Rathbun, Bull. U.S. Nat. Mus. No. 97, 1917, p. 308, pl. lxxxix.

Material examined.—One female from Gulf of Paria, Trinidad. Collected by Mr. P. H. Johnson.

Depth.—3-6 fathoms.

Measurements :—

	mm.
Distance between external orbital angles	15.0
Greatest breadth of carapace	16.0
Length of carapace	14.5
Breadth of superior border of front	8.0
Breadth of inferior border of front	8.5
Length of penultimate legs	30.0
Length of merus of penultimate legs	11.0
Breadth of merus of penultimate legs	4.0

Range.—Southern Florida to Rio de Janeiro, Brazil; Bermudas, West Indies.

SESARMA (HOLOMETOPUS) ANGUSTA Smith.

Sesarma angusta Smith, Trans. Conn. Acad. Arts. Sci. vol. ii, 1870, p. 159; Rathbun, Bull. U.S. Nat. Mus. No. 97, 1917, p. 314, pl. xxi.

Material examined.—One male from Coiba Island, Bay of Panama.

Habitat.—Embedded in sand at low water mark, among fine sea-grass and dead coral.

Measurements :—

	mm.
Length of carapace	9.5
Breadth of carapace	9.0
Breadth of frontal margin	5.0
Length of third leg	21.0
Length of merus of third leg	8.0
Breadth of merus of third leg	3.0

Range.—From west coast of Costa Rica to Bay of Panama.

Genus ARATUS H. Milne-Edwards.

ARATUS PISONII (H. Milne-Edwards).

Sesarma pisonii H. Milne-Edwards, Hist. Nat. Crust. vol. ii, 1837, p. 76, pl. xix, figs. 4 & 5.

Aratus pisonii Rathbun, Bull. U.S. Nat. Mus. No. 97, 1917, p. 323, pl. xevi.

Material examined.—One male from Gulf of Paria, Trinidad. Collected by Mr. P. H. Johnson.

Depth.—3–6 fathoms.

Remarks.—Tubercles of the hand and granules of the frontal and gastric regions are not so well developed as those described by Miss Rathbun and figured by Milne-Edwards.

Measurements :—

	mm.
Length of carapace	12·5
Breadth of carapace	13·0
Breadth of front	7·5
Height of front.....	2·0

Range.—From Florida to São Paulo, Brazil; Bahamas; West Coast of Nicaragua to Peru.

Genus *PLAGUSIA* Latreille.*PLAGUSIA IMMACULATA* Lamarck.

Plagusia immaculata Lamarck, Hist. Anim. sans Vert. vol. v, 1818, p. 247; Miers, Ann. & Mag. Nat. Hist. 1878, p. 150; Report 'Challenger' Expedition, vol. xvii, Brachyura, 1886, p. 273, pl. xxii, fig. 1; Rathbun Bull. U.S. Nat. Mus. No. 97, 1917, p. 335, pl. ciii.

Material examined.—One small male. Collected by Colonel Kelsall.

Habitat.—Floating on leguminous fruit twenty miles off land (Panama). Wind light, blowing towards land.

Remarks.—The specimen collected by Colonel Kelsall differs from the figure given by Miers in certain characters of the chelipeds and ambulatory legs. The cheliped here has a conspicuous fringe of hair on the merus, carpus, and propodus, extending to the base of the dactylus. Carpus with irregular foldings on the outer surface; propodus with three deep grooves on the upper surface, the outer one being the most marked; surface minutely punctate, outer portion of hand transversely punctate. Fingers much more slender than those figured by Miss Rathbun.

Carpus and propodus of ambulatory legs grooved. Surface of the carapace with tubercles depressed, but in some cases quite distinctly fringed with short hairs.

Measurements :—

	mm.
Length of carapace	10·0
Breadth of carapace	11·0
Breadth of fronto-orbit.....	8·5
Breadth of front	4·0
Length of cheliped.....	10·5

Range.—Indo-Pacific region: Costa Rica to Panama.

Family GECARCINIDÆ.

Genus *CARDISOMA* Latreille.*CARDISOMA CRASSUM* Smith.

Cardisoma crassum Smith, Trans. Conn. Acad. Arts. Sci. 1870, vol. ii, p. 144, pl. v; Rathbun, Bull. U.S. Nat. Mus. No. 97, 1917, p. 341, pls. cvi & cvii.

Material examined.—One male. Locality uncertain, probably Gorgona.

	mm.
Length of carapace	63·0
Breadth of carapace	76·0
Breadth of fronto-orbit.....	56·0
Breadth of front	18·0
Height of orbit	10·0
Length of orbit	18·0

GECARCINUS QUADRATUS de Saussure.

Gecarcinus quadratus de Saussure, Rev. et Mag. de Zool. ser. 2, vol. v, 1853, p. 360, pl. xii, fig. 2; Rathbun, Bull. U.S. Nat. Mus. No. 97, 1917, p. 358, pls. cxxi-cxxii.

Material examined.—Two males and three young from Coiba Island, Bay of Panama.

Habitat.—Embedded in sand at low water mark, among fine sea-grass and dead coral.

Measurements (larger male):—

	mm.
Length of carapace	32·0
Breadth of carapace	40·0
Breadth of fronto-orbit.....	20·0
Breadth of frontal margin	8·0

Range.—From Mexico to Colombia on the Pacific side; also from Atlantic side of Colombia.

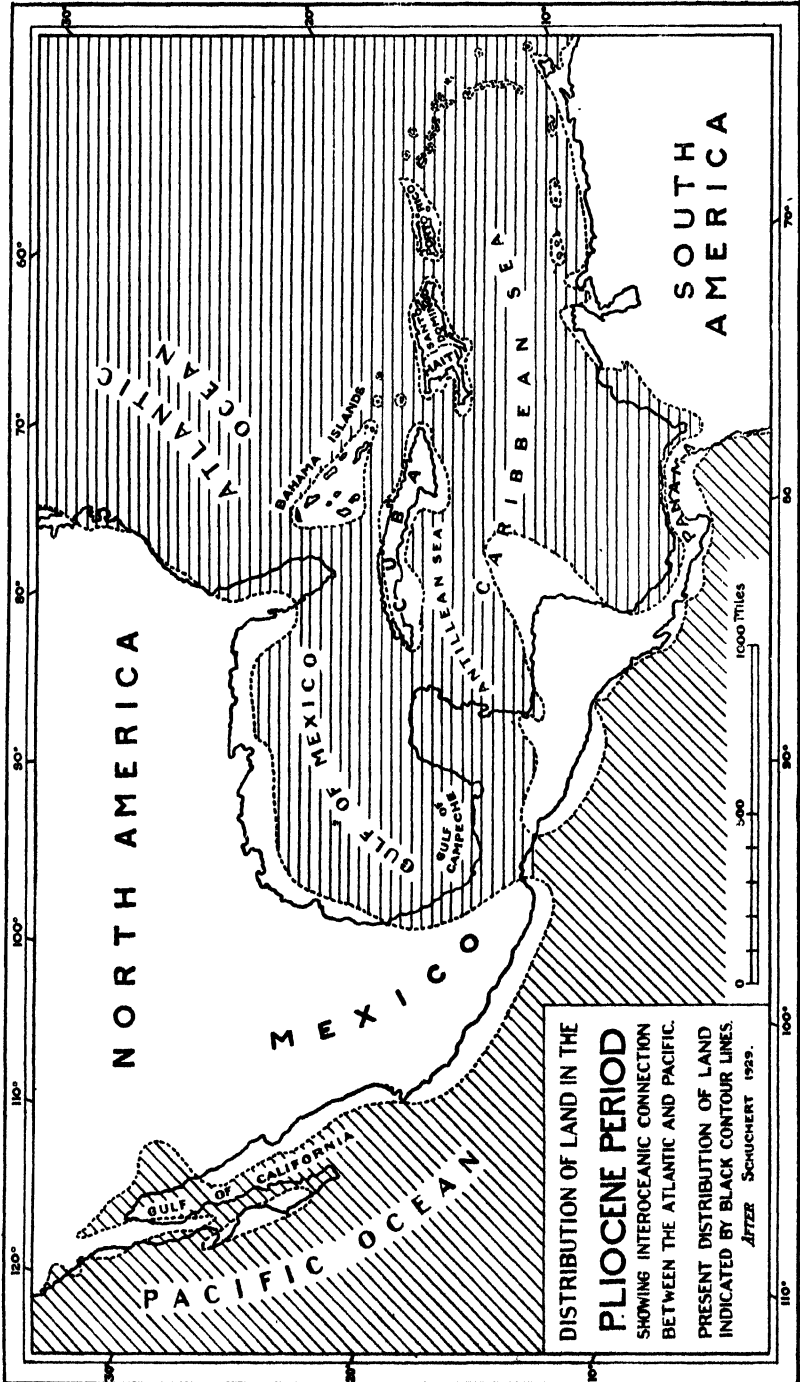
GEOGRAPHICAL DISTRIBUTION.*General Factors.*

Within the limits set by the distribution of land and water, the main factor controlling the geographical distribution of marine Crustacea is temperature. In the region of Central America the temperature of the waters of the West Coast is determined chiefly by the currents of the Pacific, and on the East Coast chiefly by the currents of the Atlantic.

The oceanographical work published by the Lords Commissioners of the Admiralty in 1923 (see Somerville) contains a diagram of ocean-currents, and the currents that would chiefly affect the temperature of the waters on the coasts of Central America can be determined from it. A simplified chart of these currents can also be seen in Chart vii, 'Science of the Sea' (see Fowler & Allen).

In the Pacific the result of these currents is that the actual oceanic heat-equator is pushed from 5° to 10° N. of the earth-equator; the temperature around the Galapagos Islands, although on the Equator, has an isocryme 12° lower than that of Panama. The waters of highest temperature occur along the coast of Mexico and Panama and from Panama southwards. On the Atlantic coast an interesting point can be seen in the Admiralty Chart; this is the apparent extension of the Labrador current beyond Cape Hatteras, southwards to the Straits of Florida, and following every convolution of the coast round

CHART II.



the Gulf of Mexico, Yucatan, Colon, to Venezuela. If the existence of this current can be substantiated, it will be of considerable importance; although south of Cape Hatteras, it differs only by 2° or 3° C. from the temperature of the Gulf Stream.

On the east coast of Central America the warmest waters are the Caribbean Sea bathing Venezuela, Panama, Yucatan, and the West Indies, which are practically of the same temperature as the Pacific in the region of Mexico and Panama. Further north the water tends to become colder more quickly and more abruptly on the Atlantic side than on the Pacific, although much the same temperature-conditions prevail within the regions that we consider. The areas where the greatest disparity occurs are on the east and west coasts of South America, where on the Atlantic side the warm waters extend as far south as Bahia to a latitude of 20° S., and on the Pacific side only as far south as Guayaquil, to a latitude of only 2° or 3° S. of the equator. In addition to their influence on the temperature of the waters, oceanic currents may sometimes affect the distribution of marine organisms by their direct action as transporting agencies.

On the Pacific coasts, with southerly currents from California driving the surface waters at the rate of 10 to 30 miles per day, we should expect to find a drifting southwards of species from the north to Manganillo, possibly to Panama, but not beyond that, owing, firstly, to the encounter of opposing currents, and, secondly, to the effect of the cold Peruvian waters. From Peru there would also be a tendency for the species to be carried towards the Panama area. On the Galapagos shores we should expect, from the set of currents, to find species from Panama as well as from Chili and Peru.

On the Atlantic coast, if the above-mentioned extension of the Labrador current actually extends as far as Venezuela, and maintains throughout its entire course a speed of 12 to 20 miles per day, it will undoubtedly have an effect on the littoral species of the entire coast.

The influence that such currents might exert on the species along an unbroken coast-line is obvious, but it is not so clear that the great trans-oceanic currents can act in a similar way. It seems incredible that the larvæ of littoral species could travel across the breadth of the Pacific even when driven by a current flowing from 30 to 40 miles per day, and allowing for the resting-places provided by the numerous islands.

The 'St. George' Collection in relation to Geographical Distribution.

Of the sixty-five species of Brachyura collected by Dr. Crossland on the early part of the 'St. George' Expedition, eight are new to science, and there is one new variety. The number of new forms is partly due to the fact that the area had not, until recently, been worked on for many years; but it is also due to the method employed in collecting the material. Numerous "washings" were taken from coral débris and sea-weeds, and narcotization was used to

liberate the smaller forms of life ; the result being that, except where the crabs were definitely sought, most of the material consists of exceedingly small specimens.

Chart 1 (after Crossland) shows the area from which this material was derived, with the exceptions of *Polybius henslowii*, which was taken in European waters, and two crabs collected at Marquesas Islands.

Seven species were taken on the Atlantic side of the Isthmus, and the rest on the Pacific side. Eleven of the species are already known, or are now recorded from both sides of the Isthmus, and thirteen of the remainder have closely allied species which have been termed " representative species " on the opposite side of the continent.

Those recorded from both sides of the Isthmus are :—

<i>Cycloes bairdii</i> .	<i>Panopeus bermudensis</i> .
<i>Acanthonyx petiverii</i> .	<i>Panopeus serratus</i> .
<i>Portunus (Achelous) spinimanus</i> .	<i>Pilumnus fragosus</i> .
<i>Portunus (Achelous) spinicarpus</i> .	<i>Pachygrapsus transversus</i> .
<i>Cronius ruber</i> .	<i>Gecarcinus quadratus</i> .
<i>Domecia hispida</i> .	

The " representative species " are :—

Pacific.	Atlantic.
<i>Calappa saussurei</i> .	<i>C. angusta</i> .
<i>Stenorhynchus debilis</i> .	<i>S. seticornis</i> .
<i>Herbstia tumida</i> .	<i>H. depressa</i> ?
<i>Hemus analogus</i> .	<i>H. cristulipes</i> .
<i>Thoe panamensis</i> .	<i>T. sulcata</i> .
? <i>Achelous brevimanus</i> .	<i>A. spinimanus</i> .
<i>Glyptoxanthus labyrinthicus</i> .	<i>G. erosus</i> .
<i>Eriphia gonagra</i> .	<i>E. squamata</i> .
<i>Actæa sulcata</i> .	<i>A. rufopunctata</i> .
<i>Actæa stimpsoni</i> .	<i>A. denticulata</i> .
<i>Actæa dorii</i> .	<i>A. setigera</i> .
<i>Platypodia rotundata</i> .	<i>P. lobata</i> .
<i>Heteractæa lunata</i> .	<i>H. ceratopa</i> .

Of these " representative species " there is evidence that two pairs, at least, cannot be considered as such, for one of each pair is now known to occur in both oceans. The specimens of *Achelous spinimanus* collected by the ' St. George ' in the Pacific bear a closer resemblance to the Atlantic form (*A. spinimanus*) than they do to *A. brevimanus*, the supposed representative of *A. spinimanus* in the Pacific. Also, it is extremely doubtful whether *Heteractæa ceratopa* of the Atlantic should be regarded as representative of the Pacific *H. lunata*, since Miss Rathbun has recorded *H. lunata* from the Pleistocene on the Atlantic side of Costa Rica. *H. lunata* may not be living on the Atlantic coast of America at the present day, but its appearance there so recently as the

Pleistocene renders it unlikely that *H. ceratopus* is to be regarded as its Atlantic representative or derivative.

In theory, the use of the term "representative species" implies either that the two forms have diverged from a common stock, or that one has been derived from the other, which itself has remained unchanged since the separation of the areas now occupied by the two species. In practice, however, we have to be satisfied if it can be shown that the two species resemble each other more closely than either does any other species of the genus. If this condition is not fulfilled, it is clearly not justifiable to term the species "representative," since either, or both, may have acquired their characters elsewhere before migrating into the areas they now inhabit.

In the 'St. George' material the most striking example of "representative species" is given by the Pacific *Stenorhynchus debilis* and the Atlantic *S. seticornis*, which can only be distinguished by the presence in *S. debilis* of a spine on the base of the second antenna: in every other respect they are identical. In most cases, however, the resemblance is less close, and the individual cases standing alone might be of doubtful significance; the very number of the cases, however, greatly increases the likelihood that the resemblances have a genetic significance. In other words, the mere fact that so many closely related species are found on the opposite sides of the Isthmus makes it impossible to avoid the conclusion that they are "representative" in the sense defined above, although it may be impossible to be quite sure of this in any individual case.

The eight new species in the collection have not extended the range of the genera to which they belong, and most of the other species were taken within the limits of their known range: but the following extensions have been observed:—

Eight species extending their range from the Gulf of California to Gorgona, Taboga Islands, etc:

<i>Calappa saussurei</i> .	<i>Leiolambrus punctatissimus</i> .
<i>Ethusa mascarone</i> var. <i>americana</i> .	<i>Portunus</i> (<i>Achelous</i>) <i>tuberculatus</i> .
<i>Herbstia tumida</i> .	<i>Xantho stimpsoni</i> .
<i>Hemus analogus</i> .	<i>Actea sulcata</i> .

Three species extending their range from Panama to the Galapagos Islands:

<i>Mithrax pygmaeus</i> .	<i>Panopeus bradleyi</i> .
<i>Platypodia rotundata</i> .	

Four species extending their range from Atlantic to Pacific coast of Central America:

<i>Portunus</i> (<i>Achelous</i>) <i>spinicarpus</i> .	<i>Panopeus serratus</i> .
<i>Panopeus bermudensis</i> .	<i>Pilumnus fragosus</i> .

The occurrence of *Trapezia cymodoce* var. *ferruginea* at Colon extends the range from the Indo-Pacific, Mexican, and Panama areas to the east coast of Central America. *Epialtus peruvianus* reaches now from Peru to the Galapagos Islands,

and *Portunus (Achelous) spinimanus*, hitherto represented on the Pacific side at Chile only, is known as far north as Gorgona Island, where its presence was to be expected.

Obviously it is impossible to generalize from the data afforded by so small a collection; but the impression that is gained is, first, that the relation between the faunas of the east and west coasts of Central America is exceedingly close; that not only are many species common to both sides, but a great number of the genera are confined to this region and have their representatives on either side of the Isthmus. Secondly, that on the Pacific coast the area from the Gulf of California to Panama may be regarded as a definite faunal unit with a number of species reaching as far west as the Galapagos Islands.

These results will be seen more clearly if the regions under consideration are extended and a complete list of their species noted.

*Regions adopted as Basis for Investigation of the American Faunas
of the Pacific and Atlantic Coasts.*

Giving the regions of primary interest in this paper the names of "Panama Region" on the Pacific (extending from Panama to Cape St. Lucas) and "Caribbean Region" on the Atlantic (extending from Colon to the Straits of Yucatan), the "Northern Area" on the Pacific was then taken to consist of the coast between Cape St. Lucas and Monterey Bay, and the "Southern Area" to consist of the coast between Panama and Guayaquil, Southern Ecuador. On the Atlantic side their analogues are from Yucatan to S. Florida and from Colon to Pernambuco. Each of these areas was in turn extended, and the following subdivisions were arrived at:—

Pacific.

Panama Region.—Panama to Cape St. Lucas.

Northern Area, with the subdivisions.—Cape St. Lucas to San Diego; San Diego to Monterey Bay; Monterey Bay to Puget Sound.

Southern Area, with the subdivisions.—Panama to Guayaquil; Guayaquil to Chinchas Islands; Chinchas Islands to Valparaiso.

Atlantic.

Caribbean Region.—Colon to Yucatan.

Northern Area, with the subdivisions.—Yucatan to Southern Florida; Florida to Cape Hatteras; Cape Hatteras to Cape Cod.

Southern Area, with the subdivisions.—Colon to Pernambuco; Pernambuco to Rio de Janeiro; Rio de Janeiro to Patos-Lagune.

These areas are not arranged in relation to isothermal lines, and are in no sense meant to represent zoogeographical regions in the strict sense. They are selected with a certain regard for the temperature of the waters within their limits, but are arbitrary divisions that seemed, judging from the results of other workers, to form a convenient basis for investigations.

General Features of the Distribution of American Brachyura.

Of the eight hundred and twenty-four species recorded in the statistical tables, the following sections have been selected and analysed :—

Total Panama species	130 (2 ?)	Total Caribbean species	60 (1 ?)	
Species recorded only from Panama Area (<i>i. e.</i> , between Panama and Cape St. Lucas). ..	52	Species recorded only from Caribbean Area (<i>i. e.</i> , between Colon and Yucatan Straits)... ..	7	
Panama species extending north to San Diego	37	Caribbean species extending north to S. Florida	26 (1 ?)	
Panama species extending north to Monterey Bay	12	Caribbean species extending north to Cape Hatteras	12	
Panama species extending north to Puget Sound	3	Caribbean species extending north to Cape Cod... ..	5	
Panama species extending north of Puget Sound	3	Caribbean species extending north to Cape Cod.....	0	
Panama species extending to Galapagos Is.	22	Caribbean species extending to W. Indies	45	
Panama species extending south to Guayaquil	6 (1 ?)	Caribbean species extending south to Pernambuco	12	
Panama species extending south to Chinchas Is.	6	Caribbean species extending south to Rio de Janeiro	9 (1 ?)	
Panama species extending south to Valparaiso	5	Caribbean species extending south to Patos-Lagune	5	
Panama species extending south of Valparaiso	3 (1 ?)	Caribbean species extending south of Patos-Lagune	0	
Species recorded only from Galapagos, Cocos, and Gorgona Islands.....	20	Species recorded only from West Indies	96	
Pacific species ranging from Northern Area to Southern Area and Galapagos Islands .	4	Atlantic species ranging from Northern Area to Southern Area and West Indies.....	57	
Species common to Galapagos and Northern Area (Pac.)	6	Species common to West Indies and Northern Area (Atl.)	69	
Species common to Galapagos and Southern Area (Pac.)	6	Species common to West Indies and Southern Area (Atl.)	8	
Species common to Northern and Southern Areas, but not re- corded from Intermediate Area (Pac.).....	4	Species common to Northern and Southern Areas, but not re- corded from Intermediate Area. (Atl.)	3	
Species occurring from Indo- Pacific Region to West America (3 to Panama)	8	Species occurring from West African Region to East America (? to Caribbean)	14	
Species occurring from Panama, East America coast to North-East Africa and Cape Verde Is.....				5
Species common to East and West America (circumtropical)				2
Species common to East and West America (not circumtropical)				27

One condition that is brought out clearly above, and that confuses the results of statistical analysis, is that the entire areas on both sides have not received an equal amount of attention, certain sections having been worked at much more than others.

The difference between the figures recorded for the species reported only from the Panama area (52) and for the species reported only from the Caribbean area (7) is probably due to such a discrepancy. But a much truer ratio is obtained in the areas north and south of them ; on the Pacific side the species from Panama are largely represented to the latitude of San Diego ; up to Monterey Bay they are still comparatively numerous ; but beyond that they fall away rapidly to Puget Sound and north of it.

On the Atlantic side the falling away is more marked, as was to be expected, and a very small proportion extend beyond Cape Cod. In the southern regions of both the Atlantic and the Pacific few Panama and Caribbean species are represented at all. The species recorded from the Bermudas are included with the West Indian Area. The number extending from the Northern to the Southern Area, and including the West Indies, is 57. In particular, the proportion reported as common to the West Indies and the Northern Area (69) is very much greater than the corresponding figure for the Pacific (6).

In view of Faxon's supposition that certain species may occur in the north and in the south, and migrate through the intermediate tropical zone by seeking greater depths, it is interesting to note that only four and three species on the two sides respectively are recorded from the north and south without intermediate links.

From Japan (coming *via* Bering Sea), seven species actually reach far enough south on the north coast of America to come under consideration here, although only one reaches Panama. Similarly, seven species round the Straits of Magellan and occur on the east and west coasts of South America within our limits, although none of them reaches the Panama and Caribbean Areas.

From the Indo-Pacific region eight species actually reach the West American Coast, but the vast majority of the Indo-Pacific forms stop short at the Marquesas and Hawaiian Islands. On the other side, from West Africa to East America, the number reported as common only to these two regions is 14. The number of species that are completely circumtropical is only two.

Distribution of the American Marine Brachyura in relation to Oceanic Currents.

Oceanic temperature, by producing favourable or unfavourable ecological conditions, limits the distribution of species, especially in a north-south direction ; in particular, a species from the warmer region has less chance of surviving in a migration polewards than *vice versa*, for the reason that the polar or temperate form has the alternative of sinking into deeper water and regaining suitable temperature.

In 1852 Dana drew up his chart to illustrate the geographical distribution of marine animals, and based his zonal divisions on "isocrymal lines." These lines he arrived at by plotting out points of equal mean temperature for the coldest thirty consecutive days of the year. But although he divided the waters into zones that were determined as accurately as possible by certain definite temperatures, nevertheless his actual zoogeographical provinces did not fall into this scheme, but ranged rather north and south with the general trend of the great continents. Faxon and others, while agreeing emphatically with him in drawing the primary divisions with reference to the isocrymal lines, take exception to his action in basing his faunal zoogeographical areas chiefly on lines running across the isocrymes.

But on p. 1488 of the same publication Dana explains his position quite logically by stating :—

"In making an application of the isothermal oceanic chart to the subject of the geographical distribution of Crustacea, we have two objects before us :

"*First*.—To compare the zones and their regions with one another as to (a) number of species, (b) number of genera, (c) number and size of individuals, (d) grade of species, in order to arrive at some general conclusions as to the temperature best fitted for the highest and most prolific development of Crustacea.

"*Second*.—To compare different geographical positions in similar regions with one another, in order to arrive at their resemblances and differences and deduce the several distinct provinces ; and also to distinguish the more or less wide diffusion of species in longitudinal range."

It must be remembered that Dana was not an evolutionist, and his standpoint with regard to the distribution of animals differs from ours in that he does not contemplate a historical development of faunas. Allowing for this, however, it is clear that the first of the two objects mentioned might be defined in modern terms as the study of ecological distribution, while the second is essentially the study of those facts that nowadays find a historical explanation.

Faxon, however, being convinced, as are most other carcinologists, that temperature is the fundamental limiting factor in the distribution of species, brings this part of his argument to the following conclusion :—"But, on the whole, the change of temperature encountered in passing from low to high latitudes has proved a barrier to the migration of species of tropical littoral types northwards . . . a more effectual barrier, it would seem, than the immense distances between the tropical shores of the different continents have proved to be against the intertropical dispersal of such types around the globe. Every summer myriads of delicate larvæ, belonging to tropical and subtropical genera, such as *Ocypode* and *Calappa*, are borne on the warm bosom of the Gulf Stream to the southern shores of New England only to perish on the approach of the northern winter. Yet these same genera are represented by flourishing colonies established on tropical shores around the whole girdle of the globe."

In this Faxon was undoubtedly correct, but while temperature is the chief

barrier in limiting distribution in a north-south direction, it can only explain certain features of the problem, as an analysis of the American tropical and subtropical faunas indicates quite clearly.

If Dana's primary zones, based on isocrymal lines, were bounded by continents running in an east-west direction, then a general spread of the species all around the circumterrestrial belt would undoubtedly follow, provided no new impediment to migration arose. But the trend of the continents is north-south, not east-west, and for uniform temperature inducing suitable ecological conditions we have to look to the Indo-Pacific region, Central America, the west and east coasts of Central Africa, and so on, that is, at the present day, the species that migrates along these natural lines is faced with two insurmountable barriers—land and water. Of the species of crabs inhabiting the coasts of Central America, an exceedingly small proportion extends across either to India or West Africa.

Currents, as means of transport, are aids to migration, and may conceivably account for the diffusion of Indo-Pacific forms from the Marquesas Islands to the Indian coasts. It is, however, highly improbable that the entire gap from India to Central America can be bridged in this way, and the facts are quite against it, as can be seen by the difference between the faunas of the Marquesas Islands and the west coast of Central America alone. Where currents can act as effective vehicles of transport is along unbroken or practically unbroken coast-lines, but here again we have the difficulty of a north-south migration, namely, temperature. In this connection it is interesting to observe that the species found between, say, 37° N. and 8° N. make comparatively little headway north or south of this, but in the regions of higher latitude the range is very much extended. For examples, take the eight species recorded at intervals along the connecting coast-line between Japan and the temperate portion of the west coast of North America and the analogous occurrence in the southern hemisphere of the seven South American species rounding Cape Horn and extending up the east and west coasts to practically the level of the earth-equator.

In spite of the fact that comparatively few species are circumtropical, Faxon was right in maintaining that the faunas of the tropical regions were closely allied to one another, and Dana also was right in basing his quantitative analysis along isocrymal lines; but it is the genera, not the species, that make this fact evident.

The entire circumtropical, or the Indo-Pacific-American and American-African faunas are knit together not so much by their species as by their genera. The significance of this is that, while the genera have their greatest spread in an east-west direction, the species tend to range in a north-south direction. From the conclusions that have gone before, the explanation would seem to be that genera, being much older than the species, were established at a period when the barriers now in existence, such as the Isthmus of Panama etc., did not impede their migration.

The species, however, arising later succeeded to a small degree in extending their range in the only direction that was possible for most littoral forms—that is, along the line of the continental shores.

They penetrate to the limit where the ecological conditions are most suitable, and within those limits where the temperature is favourable, or not unfavourable enough to eliminate the species, currents do play a part in transporting the larval forms to new territory.

As far as concerns the small, but not negligible, percentage of Indo-Pacific forms that actually reach the West American coast and West African forms on the East American coast, we look to geological evidence to supply the explanation.

Whether we accept Ortmann's hypothesis of a former circumtropical land-belt or Wegener's more recent suggestions is for geologists to decide.

The Atlantic and Pacific Faunas of Central America in relation to former Inter-oceanic Connections and Land-bridges.

Finally, the characteristics of the faunas of the east and west coasts of Central America can only be understood and interpreted in the light of the palaeogeography and palaeontology of that region.

Florida and the neighbouring Southern States, together with the Antilles and Central America, have constituted a mobile portion of the earth's crust extending between North and South America, sometimes forming a complete bridge, at other times broken and leaving a connecting channel between the Atlantic and Pacific Oceans. Professor Wayland Vaughan gives the periods of interoceanic connection as Upper Eocene, Middle and Upper Oligocene, Lower Miocene, and (a narrow connection) very late Miocene or Pliocene times (see Chart II, indicating the most recent connection of the Pliocene period).

Other important changes that have taken place are the formation and deepening of the Gulf of Mexico and the breaking down of the former land-connection between Central America and the Antilles. The Gulf of Mexico is situated on a sunken part of the extensive "flat-plate" or "foreland" of the Greater Antilles and Central America, and has attained its present depth and size only since Cretaceous times. The other part of the "foreland," connecting Central America and the Antilles, persisted more or less intact till the Upper Eocene period, since which time its association with the mainland has been incomplete or entirely cut off.

These facts explain the similarity of the faunas of the east and west coasts of Central America and their relation to the fauna of the Antilles.

In this connection it is interesting to contrast the relationship of the faunas of the west coast of America with its outlying islands, the Galapagos. These islands, from which much of the 'St. George' material was derived, are probably volcanic in origin, with no continental connection. Baur, from his work on the fauna and flora of these islands, contended that he found the fauna to be what he called "harmonic," that is, harmonizing with the fauna of the adjacent

continent, and from these results he drew the conclusion that the islands were "continental." But recent work done by Chubb on the geology of the Galapagos supports Darwin's earlier theory that the islands are of volcanic origin. Evidence from the Brachyuran faunas is too incomplete to be cited with certainty, but the available data suggest that there are relatively fewer forms common to the Galapagos Islands and West America than there are common to the Antilles and Central America. Too much stress, however, cannot be laid on this, for the temperature of the waters around the Galapagos is about 12° lower than that of the Panama waters.

Professor Wayland Vaughan, after studying both the fossil and recent corals of Central America, states :—"Comparisons of faunas according to the percentage of species in common may be very misleading. Faunas now living only a short distance from each other may have nothing or almost nothing in common."

Therefore, before accepting the results obtained by a comparison of the living Brachyura of the Pacific and Atlantic coasts of the Panama region, it will be well to ascertain what support or modification will result from an examination of the data afforded by palæontology.

There is very little evidence available for this purpose : beyond a few isolated papers, the most comprehensive works have been those published by Miss Rathbun on the fossil forms from the Pacific Slope, from Panama, and from the West Indies.

Most of the material is from the Pliocene and Pleistocene Series, and a great number of the species are represented to-day in the American fauna. A rough calculation shows that of the total number of fossil crabs recorded from these regions, approximately 26 per cent. are recent species and 74 per cent. (including the recent species) belong to the recent genera.

The genera that are regarded as typically or exclusively American, like *Mithrax* etc., as a general rule are recorded only from as far back as the Pleistocene or Pliocene periods, although one notable exception, at least, is the genus *Panopeus*, which dates back as far as Cretaceous times. On the other hand, the older genera, where they have living representatives at all, usually show a much wider distribution.

In this connection a most important point is established, that is, the greater similarity in the past of the Indo-Pacific and Central American faunas. Miss Rathbun records a species of *Thaumestoplax* from the Oligocene of Panama : this is a crab belonging to the Hexapodinae, a small group not previously recorded in the fossil state, and now living exclusively in the Indo-Pacific region. Professor Wayland Vaughan also lists a number of genera of fossil corals found in Central America and representing again a branch of what is considered to be the Indo-Pacific fauna.

Further, the palæontological evidence, so far as it goes, supports the statement made in the preceding chapter : that genera, where they have had time to spread, distribute themselves in an east-west direction, while species, being younger, and having had less time to disperse, tend to range in a north-south direction.

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Relative Growth of Mandibles in Stag-Beetles (Lucanidae)*. By J. S. HUXLEY, M.A. (Oxon), F.L.S., F.Z.S., Honorary Lecturer in King's College and Fullerian Professor of Physiology in the Royal Institution.

(With 9 Graphs.)

[Read 5th November, 1931.]

(1) INTRODUCTION.

In previous papers (Huxley, 1927 *b*, etc.) I have shown that when an organ shows a growth which is disproportionate to the body as a whole (heterogonic growth, in the useful term of Champy, 1924), the relation between it and the rest of the body can be in some cases expressed by the formula $y = bx^k$, where y = size of organ, x = size of body, and b and k are constants. This has been shown to hold good with great exactitude for the weight of the large chela in fiddler-crabs (*Uca*) and for numerous other organs in other forms. It is theoretically the simplest way in which disproportionate growth can be brought about, since it implies that the proportion between rate of growth of organ and rate of growth of the rest of body remains constant, this constant being, of course, represented by k in the above formula (see also Pearsall, 1927, who has arrived at similar conclusions in plants). This formula I therefore propose to call the *simple heterogony formula*. The value of k then represents the *growth ratio* of the two organs considered: or, where one organ is always taken as the standard of comparison, it can conveniently be called the *growth-coefficient* of the organ regarded as variable. The formula may be modified in numerous ways—it may only hold for a short period of life, the expected values may be prevented from being realized for special physiological or mechanical reasons, etc., but it appears to remain the common basis throughout. A peculiar special case is seen in holometabolous insects. It has long been known that the males of many of these, notably among Coleoptera, possess heterogonic appendages, usually either cephalic or thoracic "horns," or mandibles. Other organs, however, may also show heterogonic growth, such as antennæ, legs, etc. Champy (1924) has collected a number of instances in his book. The peculiarity of the matter here is, of course, the fact that there is no continuous heterogonic growth, but that the disproportionate organ appears suddenly in the imago only.

In a preliminary communication (1927 *b*) I have shown that the simple heterogony formula applies to the mandibles of Lucanids, and elsewhere (1927 *a* and 1927 *c*) that it is in all probability the basis underlying the curious phenomena shown in the bimodal curves for the forceps of the earwig and the horns of the beetle *Xylotrupes*.

* 'Studies in Heterogonic Growth,' ix.

The purpose of this paper is to present the data for *Lucanidæ* more fully, in the hope that entomologists may be induced to undertake further work upon this subject.

(2) *I. LUCANUS CERVUS*.

Mr. H. H. Brindley, of St. John's College, Cambridge, has kindly furnished me with the original data on which the information given in Bateson and Brindley's paper (1892) is based. In that paper the authors give frequency curves for mandible-length and total length separately, but give neither the individual measurements, nor any analysis of the relation between the two characters. *A propos* of this it might be pointed out how desirable it is to publish data *in extenso*, as well as the conclusions based upon them. Brindley's laborious measurements proved to be as serviceable for my purpose as for his original purpose : but had it not been for the good fortune that the original slips had been preserved for over a third of a century, the work would have had to be done again.

The measurements were made on 115 specimens collected in one locality in Surrey in June 1891 and June 1892. Of these, however, only 48 were made both on elytron (the measurement of length chosen to stand for body-length) and mandible. The measurements were made usually to the nearest millimetre, occasionally to 0.5 mm. For convenience, they may be tabulated by classes (Table 1). It is here worth noting, as a point of method, that we shall obtain different curves, when plotting mandible-length against elytron-length, according as we arrange our classes by elytron length or by what may be called "total" length, *i. e.*, the sum of elytron+mandible-length : the latter curve mounts at a steeper angle than the former. At first sight this fact seems surprising, but it is, of course, due to the circumstance that at the bottom of the curve, among the smallest specimens, an individual with relatively very long mandibles would be classed in *elytron class* (n), but in the "total length" class ($n+1$) ; while at the top the converse will be occurring, occasional individuals with relatively short mandibles coming in a later class when classified by elytron length than they would when classed by "total" length.

Theoretical considerations make it clear that, if taking class-means is desirable, *classification* had better be by total size, at any rate in homometabolous insects. For in these, it is the total bulk at the end of feeding-up which is of importance : during the larval period the heterogonic organs have not yet appeared, and cannot influence the ingestion of food or its distribution within the system. We therefore should consider the variation in mandible-size relative to the total length at pupation, and not to the size of the body less that of the heterogonic organ in the imago.

These considerations, however, do not necessarily apply to organisms like Crustacea with heterogonic organs present continuously during growth. For though, on the one hand, it is possible to argue that it is *total bulk* which sets

the biological limit to the size of the species, yet it is clear that of two half-grown individuals (say, in *Uca*, the fiddler-crab) of the same total bulk, one with a relatively large chela weighing 40 per cent. of the rest of the body, the other with a relatively small chela weighing 30 per cent., then the former will have, relative to its total bulk, poorer power of locomotion, smaller jaws, and smaller digestive surfaces. It therefore in these cases is certainly justifiable to classify by the "rest of the body," on which ingestion and assimilation and therefore growth depends.

TABLE 1.—Relative mandible size in 48 male *Lucanus cervus*
(Brindley and Bateson material).

Classes by <i>elytron</i> -length.				Classes by "total" length = (elytron + mandible-length).			
Class.	No. of Specimens.	Mean elytron length.	Mean mandible length.	No. of Specimens.	Mean elytron length.	Mean mandible length.	Mean "total" length.
1.....	1	mm. 25.0	mm. 6.0	1	mm. 25.0	mm. 6.0	mm. 31.0
2.....	5	30.8	8.0	4	30.87	7.75	38.65
3.....	8	31.81	9.5	5	31.5	9.0	40.5
4.....	5	32.6	10.4	10	32.55	10.0	42.55
5.....	6	33.92	11.0	5	33.8	11.2	45.0
6.....	7	35.0	12.0	7	35.07	11.86	46.93
7.....	10	36.35	12.5	11	36.36	12.82	49.18
8.....	2	37.75	13.5	5	39.2	14.4	53.6
9.....	4	39.5	14.5

The values of k are as follows, neglecting the last three points for reasons indicated in text, and the single aberrant smallest specimen :—

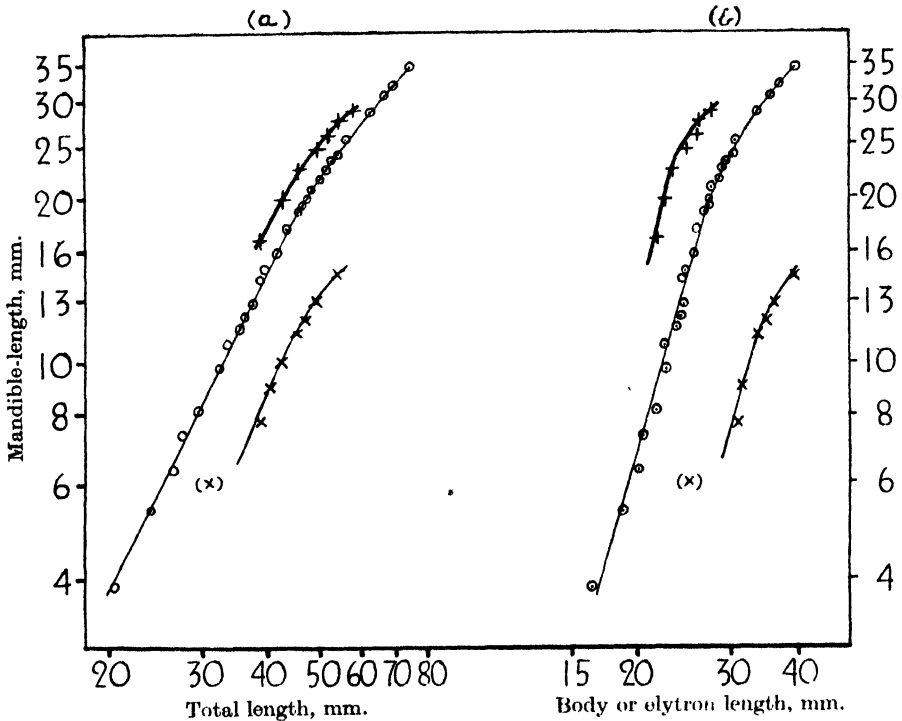
(A) for mandible-length against elytron-length when classified by "total" length classes : k = approx. 3.8.

(B) for mandible-length plotted against "total" length and classified by "total" length : k = approx. 2.3.

In any case, however, if classes are small, and classification is by "rest of body" (or any isogonic organ) and not by "total" size, the extreme classes may tend to give a false picture, the smallest size class in holometabolous insects containing too many individuals with relatively large heterogonic organs, and therefore absolutely small bodies, the largest size class, in other types as well as insects, comprising too many specimens with relatively small heterogonic organs, since the individuals are here approaching the upper limit of total size.

It might be urged that in holometabolous insects we should not only classify by total size, but actually *plot* heterogonic organ against total size instead of against rest of body. This could be justified as follows. Since the heterogonic organs only appear during the pupal period, when no total growth is going on, they must be determined by some cause dependent on previous growth. The simplest explanation is to assume that some substance needed for their formation is accumulated during larval growth, or its later phases, at a heterogonic rate. But this substance, it may be urged, might

TEXT-FIG. 1.



Mandible-length in three species of Lucanidae, against (a) "total" length, (b) elytron-length (in *Lucanus*) or body-length (in *Cyclommatus*). Logarithmic plotting. \times , *Lucanus cervus*; +, *L. lunifer*; \odot , *Cyclommatus tarandus*.

just as well be produced by the body as a whole as by part of it, and in any case, even if produced only by a part, that part will presumably be approximately isogonic, so that the hypothetical substance will be in proportion to the total final larval size, *i. e.*, to the total imaginal size, and not to the imago's "rest of body," the size of which is not directly proportional to larval final size, but must bear a negatively heterogonic relation to it: $-y = bx^k$, where $k < 1$.

If these considerations are relevant, then double logarithmic plotting of heterogonic organ against total size should give a straight line, whereas that

of heterogonic organ against rest of body should give a curve concave upwards and to the left.

It is, however, seen from the graphs (text-fig. 1) that both methods of plotting give a curve which is concave downwards to the right (as expected, the curve where "total" length is used inflects earlier), *i. e.*, in neither case are the full theoretical values of y realized, assuming that the formula $y = bx^k$ represents the theoretical relationship. In support of the view that plotting should be against "total" size, we find that the curves thus constructed are more regular (text-fig. 1).

How are we to account for this? I think that the condition during metamorphosis may suffice to explain it. The formation of heterogonic organs in holometabolous insects occurs under nutritive conditions quite different from those obtaining in ametabolous insects or Crustacea. In the latter cases the system is open, new food-material coming in continuously, and no relative increase in the organ is possible without absolute increase of total bulk; whereas in the former case the system is closed, the heterogonic organ is formed in a few days or weeks instead of months or years, and the growth of the heterogonic organ depends on the partition of the available fixed amount of nutriment among the competing parts of the system. It is obvious that in these two sets of conditions, *time* will play a different rôle. If the rate at which actual growth of the heterogonic organ can proceed is not rapid enough, the rest of the body will have exhausted the available nutriment before the theoretically possible size of the organ has been attained, and this will become more and more marked the larger the size of the organ should theoretically have been.

Very similar conditions are seen in amphibian metamorphosis. During normal development of Anura, the limb-buds are growing continuously in an open food-system. If, however, thyroid is administered artificially, no further food is taken in, and the rapid increase of the limbs has to occur in a closed system. If the dose be strong, full limb-development is not attained by the time the rest of the metamorphosis is complete, for the sole reason that the growth and differentiation of the limbs takes too much time.

Further, apart from rates of growth, it is to be expected that there will be difficulties in the way of the organ, if very large, drawing on supplies in distant parts of the body in proportion to its theoretical demand.

For these and other reasons it is to be expected that the size of heterogonic organs in holometabolous insects will fall progressively more and more below the theoretical size expected according to the equation $y = bx^k$, with increasing absolute total size. And this, as a matter of fact, is the case in all the insects I have so far been able to examine—the disparity between actual and theoretical appearing to increase disproportionately at great size. These conclusions are entirely supported by the facts in *Cyclommatus tarandus* (see section 4 of this paper)*.

* See the Postscript to this paper (p. 702) for another possible suggestion.

Theoretically I consider that in these forms the heterogonic organ should probably be plotted against total size, and not against "rest of body," though in the present state of our knowledge this is not certainly so. In any case, it is, I think, clear (1) that even in insects such as the stag-beetle, heterogonic organs exhibit an approximation to the empirical and theoretical law found for animals with continuous growth ; (2) that further light on the subject will best be obtained by experiment. With regard to this latter point, it is unfortunate that these insects are usually inconvenient for experimental work. Possibly some tropical forms will be found suitable.

The only other writer who has dealt with this question is Champy (1924). On p. 139 Champy gives the figures for elytron-length and mandible-length in eight male specimens of *L. cervus*, and on p. 150 a curve roughly representing volumes of mandibles and body posterior to front elytron margin, the volume being taken as proportional to (length \times breadth \times depth). His length measurements, rather surprisingly, give far higher relative mandible-lengths than Brindley's here dealt with, the points falling almost on my curve for *L. lunifer*. This may be a case of geographical variation, or he may have made his measurements differently from Brindley. As to the slope of his curve, the numbers are too few to justify any statement, save that it approximates to the curves obtained by me.

(3) *LUCANUS LUNIFER.*

Through the kindness of Professor Poulton, I was able to measure a number of male *L. lunifer* from the Hope Department, Oxford. These came from several localities, so that the material is not so homogeneous as that of *L. cervus*. The numbers also are small (eighteen in all). However, in spite of these defects, the material shows some interesting points.

Maximum elytron-length was taken as indication of body-size. Not only was mandible-length measured, but also the maximum breadth and depth of the main "beam" of the mandible : and also head-breadth. "Total" length can be obtained as in *L. cervus*. In addition, a measure of mandible volume can be obtained by multiplying length, breadth, and depth, and the cube root of this should be the most satisfactory linear measure of mandibular size.

When mandible-length is plotted against "total length" (by total length classes) a curve very similar to that obtained for *L. cervus* is the result—curving over towards the high end so that the actual mandibular length falls progressively more and more short of the theoretical. The falling short appears to be a little greater than in *L. cervus*.

The actual value of k for the first part of the curve can only be given approximately for such small numbers : it is about 3.7 against elytron-length, about 1.55 against total length.

When classifying by "total" length, the following classes are obtained :—

TABLE 2.—Relative mandible-length in 18 male *Lucanus lunifer*.

Class.	No. indivs.	Classes total length.	Mean "total" length.	Mean elytron length.	Mean mandible length.	Mean mandible breadth.	Mean mandible depth.
1.....	1	mm. 38-41	mm. 38.6	mm. 21.8	mm. 16.8	mm. 1.8	mm. 1.6
2.....	2	42-44	42.4	22.5	19.9	2.4	2.0
3.....	2	45-47	45.7	23.3	22.4	2.3	2.1
4.....	3	48-50	49.3	24.8	24.5	2.6	2.3
5.....	2	51-52	51.9	25.9	26.0	3.0	2.7
6.....	5	53-54	53.8	26.1	27.7	3.0	2.6
7.....	3	55-60	57.3	28.5	28.8	3.3	2.8

We may also classify by elytron length and calculate mandible "volume" thus :—

TABLE 3.—Relative mandible "volume" ($l \times b \times d$) in *L. lunifer*.

Class.	No. indivs.	Elytron length, classes.	Mean "total" length.	Mean elytron length.	Mean mandible length.	Mean $\sqrt[3]{\text{mand. vol.}}$	$\sqrt[3]{\text{mand. vol.}}$ elytron l. per cent.	head br. elytron l. per cent.
1.....	4	mm. 21-22	mm. 42.2	mm. 22.1	mm. 20.1	4.34	19.1	70.4
2.....	3	23-24	48.0	24.4	23.7	5.12	21.0	72.2
3.....	4	25	52.0	25.5	26.4	5.74	22.6	74.7
4.....	4	26	53.6	26.3	27.4	6.03	22.9	76.3
5.....	3	27-30	57.3	28.5	28.8	6.46	22.6	75.9

When the percentage ratios of head-breadth to elytron-length are calculated for the elytron-length classes, it is found that they change in a very similar way to the ratio of $\sqrt[3]{\text{mandibular "volume"}}$: elytron-length, but not nearly so rapidly (Table 3). Both increase in passing from class 1 to 5 : the figure for the head-breadth ratio increases by under 8 per cent. of its initial value, that for the ratio of $\sqrt[3]{\text{mandible volume}}$ by over 18 per cent. This indicates that the heterogonic increase in the mandibles is in some measure passed on to adjacent structures (*cf.* male chela and walking-legs in *Maia*, Huxley (1927 b), and in *Palæmon*, Tazelaar, 1930).

The percentage ratios of $\sqrt[3]{\text{mand. vol.}} : \text{mand. l.}$ increase slightly but regularly with increasing size (from 216 to 224 per cent.). This would imply an additional reason for the bending over of the curve when mandible-length is used as measure of mandible-size: but since, when the cube root of the volume is plotted, the curve is still concave below, this cannot account for the whole of the discrepancy. It must again be supposed either that the theoretical growth-ratio alters at large sizes, or, more probably, that mechanical and physiological reasons prevent it being fully realised when the mandibles are very large, as was found probable for *L. cervus*.

(4) *CYCLOMMATUS TARANDUS* THUNBERG.

Numerous measurements of this species of Lucanid have been made by Dudich (1923), to whose paper I refer the reader for the complete original data.

The body-length (not the elytron-length) was here itself measured from the point of the epistome to the point of the elytra. The mandibles were measured from the inner basal angle to the free tip (straight, not along the curve).

For the reason given above, I have adopted the total length (= body-length + mandible-length) as the unit of *classification*. The last few columns of Table 4 give the total length, the mandible-length, and the body-length for the 28 classes. In the male the body-length of the 178 specimens measured varies from 16.39.5 mm., with mean 24.47 mm. (*i. e.*, a range of about as much as the mean); the mandible-length varies from 3.75-34.4 with mean 16.47 mm. (*i. e.*, a range of nearly double the mean!); its percentage ratio to total length varied from 23.43 to 87.87 per cent.; and the total length varied from 19.75 to 74.0 mm. Thus clearly the extent of variation in relative male mandible-size is much greater than in the two species of *Lucanus*.

The variation of the female body-length is 16 to 25 mm., with mean 20.42—*i. e.*, the female is considerably smaller than the male, and apparently less variable; however, since the male body should show negative heterogony relative to total weight, and total length will certainly not be proportional to total weight, the only satisfactory measure of difference in variability between the sexes would be total weight, which Dudich has not taken.

We will begin by taking all data for the males together. When double logarithmic plots* are made of mandible-length against (a) total length and (b) body-length, it is seen that the former is the more satisfactory, since with the latter the curve is less regular, and tends to be concave upwards for its first portion, which is theoretically unlikely, while with the former the same region of the curve is an excellent approximation to a straight line. This is in accord with the theoretical views previously set forth. Both curves become bent downwards (concave below) towards the upper size-limit. The curve of mandible against body-length is thus slightly inflected (S-shaped), showing that the failure of the mandible to reach its theoretical size becomes

very considerable at large sizes, sufficing even to invert the original shape of the curve. On this curve especially, but on both quite definitely, the progressive increase in the amount by which the mandible's growth falls short of theoretical expectation is well shown (see previous discussion under *L. cervus*).

The values for k in the simple heterogony formula for the lower part of the curve is about 3.45 when mandible is plotted against body-length; when plotted against total length it is 1.97, with the value of b just above 0.01; in both cases, classification is by total length.

Some of the most interesting considerations arise where we come to the various taxonomic forms into which Dudich considers the species should be divided. He classifies the males according to their mandibles into five main types, some of these having subtypes. They are as follows:—

- (1) *Prionodont*.—The whole length of the mandible beset with teeth.
 - (a) forma *brachygnatha*; smallest specimens procurable (prebasal teeth very poorly developed; subapical teeth not sharp).
 - (b) Prebasal teeth well defined, taking up 50 per cent. of the mandible-length in small specimens, 60 per cent. in large. Subapical teeth sharp.
- (2) *Amphiodont*.—Similar to (1), but with toothless gap between the prebasal and subapical teeth; with increasing mandible-length, this gap increases in size, and the prebasal teeth become reduced.
- (3) *Telodont*.—No prebasal teeth. The most proximal of the subapical teeth becomes enlarged, progressively, with increased absolute mandible-size.
- (4) *Mesodont*.—With a new tooth, the submedian, arising on the ventral side, with medianly directed point.
 - (a) *promesodont*. Submedian tooth small, invisible from above.
 - (b) *eumesodont*. Submedian tooth larger, visible from above.

(Dudich shows conclusively that the submedian tooth is a new formation, not homologous with the most distal of the prebasals.)
- (5) *Mesamphiodont*.—With two sets of new teeth formed in the prebasal region. One set is in homologous position to that of the submedian tooth; these are small, and decrease in size basipetally. The other set is in the same position as the original prebasals of types (1) and (2); these increase in size basipetally, and are irregular.

These five types (or seven, if we include the subtypes) succeed each other as the mandibles become larger. This is clearly seen in the table, the largest prionodont, for instance, having a body-length of 23.5 mm., the smallest mesamphiodont, on the other hand, having one of 25.5 mm.

This at once raises the suspicion that the different forms have no taxonomic significance, but are merely growth-forms, the increase in size of the mandible being automatically accompanied by the sequence of morphological changes exemplified in the forms. This suspicion is increased by the fact, freely admitted

Cyclommatus tarandus (data of Dudich), for the
the 6 growth-forms separately.

Eumesodont.			All Mesodont.			Mesamphiodont.			Total.			Mean elytron length.	Class No.
No.	Total length.	Mand. length.	No.	Total length.	Mand. length.	No.	Total length.	Mand. length.	No.	Total length.	Mand. length.		
	mm.	mm.		mm.	mm.		mm.	mm.		mm.	mm.	mm.	
..	2	20.38	3.88	16.50	1
..	5	24.01	5.31	18.70	2-3
..		26.38	6.33	20.05	
..	4	27.76	7.32	20.44	4
..	5	29.65	8.17	21.48	5
..	11	32.20	9.73	22.47	6
..	10	33.11	10.71	22.40	7
..	7	35.01	11.49	23.52	8
..	1	35.70	12.50	6	36.13	12.08	24.05	9
..	1	36.50	13.00	6	37.32	12.73	24.59	10
..	2	37.55	13.30	6	38.44	14.11	24.33	11
2	38.35	14.25	7	38.46	14.18	9	39.20	14.70	24.50	12
..	3	39.17	14.83	5	41.34	15.84	25.50	13
6	41.24	15.83	6	41.24	15.83	2	41.68	15.88	8	43.22	17.39	25.83	14
6	43.02	17.01	6	43.02	17.01	10	43.34	17.63	16	45.51	18.83	26.68	15
..	10	45.51	18.83	10	46.32	19.19	27.13	16
1	46.00	18.50	1	46.00	18.50	9	46.36	19.27	10	47.28	19.92	27.36	17
..	9	47.28	19.92	9	48.40	20.79	27.61	18
..	9	48.40	20.79	9	50.04	21.53	28.51	19
..	6	50.04	21.53	6	51.50	22.54	28.96	20
..	6	51.50	22.54	6	52.50	23.25	29.25	21
..	6	52.50	23.25	6	54.23	23.96	30.27	22
..	5	54.23	23.96	5	56.01	25.38	30.63	23
..	4	56.01	25.38	4	62.06	28.49	33.57	24
..	7	62.06	28.49	7	66.06	30.69	35.37	25
..	4	66.06	30.69	4	69.00	32.00	37.00	26
..	1	69.00	32.00	1	74.00	34.50	39.50	27
..	1	74.00	34.50	1				28

by Dudich, that there is no absolute distinction between the various forms, the classification being purely arbitrary, *e.g.*, a specimen is called amphiodont when the gap between the prebasal and subapical teeth is considered larger than the normal gap between any two teeth. Dudich says (p. 68), "Es gibt Exempläre in meinen Material, bei denen dieses Intervall kaum grösser ist als die, die präbasalen Zähne voneinander trennenden Lücken und von dieser Form an nimmt die Länge des Intervalls gleichmässig zu." The same holds good for the distinction between other forms.

Why then does Dudich believe that the forms have a real biological meaning? The answer is (1) because he finds (as is clearly shown in my Table 4) that the different forms classified by mandible-type are transgressive as regards their body-length, (2) because while the variation curve for the body-length of the females approximates to a normal frequency distribution, that for the body-length of the males does not, but is (*a*) asymmetrical (greater frequencies on the smaller side of the mode) and (*b*) tends to be multimodal, with main mode at 27 mm., and at least 4 if not 5 or 6 minor modes (Dudich's fig. 3).

As regards the first point, Dudich says (p. 75), "Die transgressive Variation macht es unmöglich, bei dem ♂ des *Cyclommatus tarandus* die in den Lucaniden-literatur überall üblichen, aber nichtssagenden dimensionellen Formen wie *F. minima*, *minor*, *media*, *major*, *maxima* aufzustellen."

Leaving aside for the moment Dudich's second point, I would like to insist here that his reasoning on the first point is not only invalid, but that such a transgressive variation of body-length among morphologically distinct mandible forms is definitely to be expected, even if the mandible forms are merely growth-forms. The only postulate we have to make is for some variability in the degree of heterogony of the mandibles; and this is well established in other types, such as fiddler-crabs.

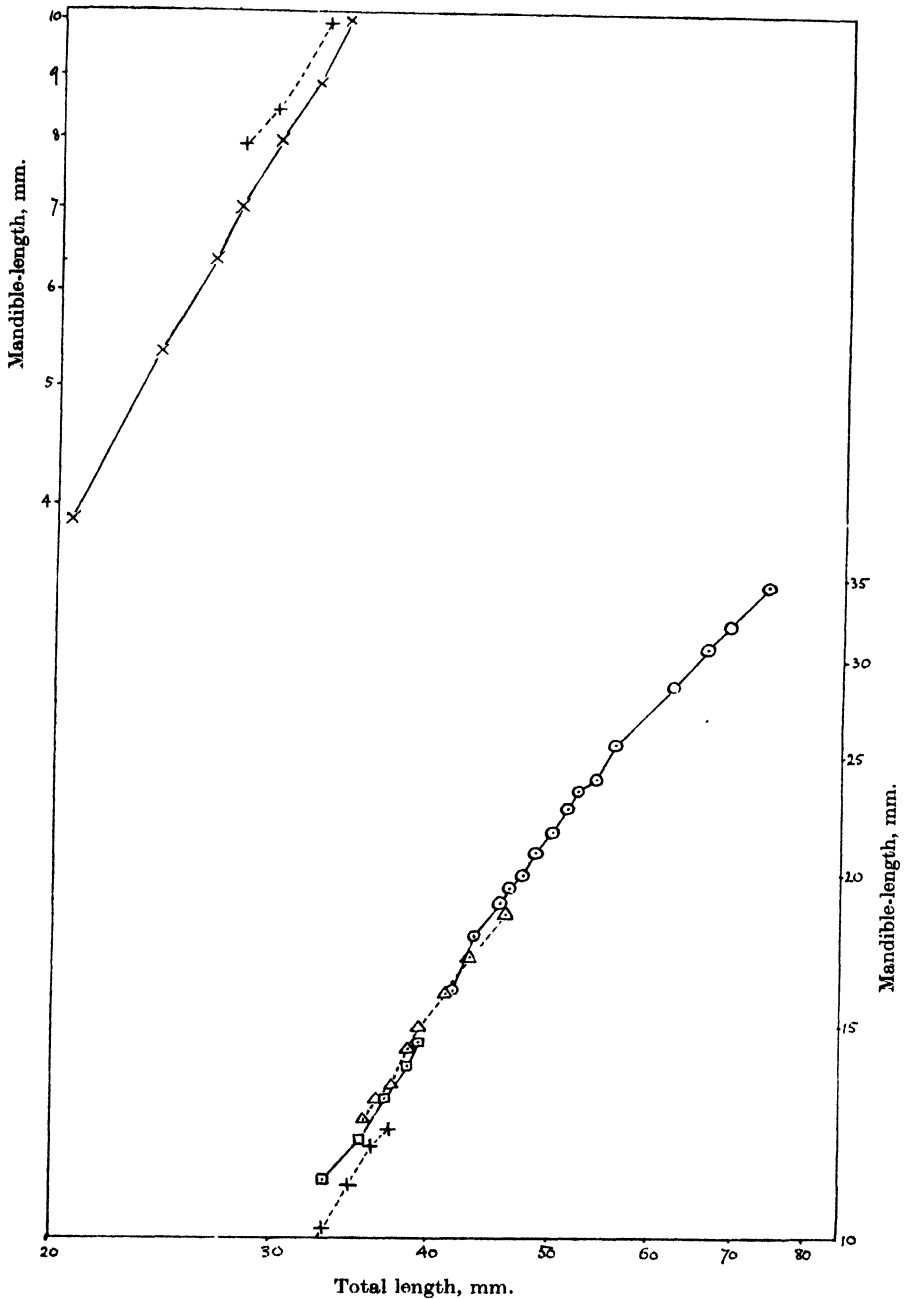
In fiddler-crabs, for instance, the size of the large claw relative to the body may vary by over 10 per cent. at a given body-size, the variation appearing to be due mainly to variation in the constant *b* in the simple heterogony formula.

If this were so with the mandibles of *Cyclommatus*, and if their morphological appearance were a function of their size, then, at the body-sizes where two "forms" overlapped, the normally expected variation would ensure that a considerable range of relative mandible-size should exist; and further on the assumption that mandible-form was a function of mandible-size, we should expect to find that the smaller-mandibled individuals should belong to one form, the larger-mandibled to the other.

That this is the explanation is made highly probable by plotting the *means* for the mandible-lengths of the different forms separately, but on one graph against body-length. It is then found that in the overlap region the earlier (smaller) form has the smaller mandibles, so that the curves overlap like tiles on a roof (text-fig. 2).

If single individuals are plotted (graph not reproduced), it is found that some single amphiodonts, for instance, have smaller mandibles than some single

TEXT-FIG. 2.



Cyclommatus tarandus.

Mean mandible-length against mean total length for the five growth-forms separately.

Logarithmic plotting. ×, prionodont; +, amphiodont; □, teleodont; △, mesodont; ○, mesamphiodont. The curve begins above to the left and is continued below to the right.

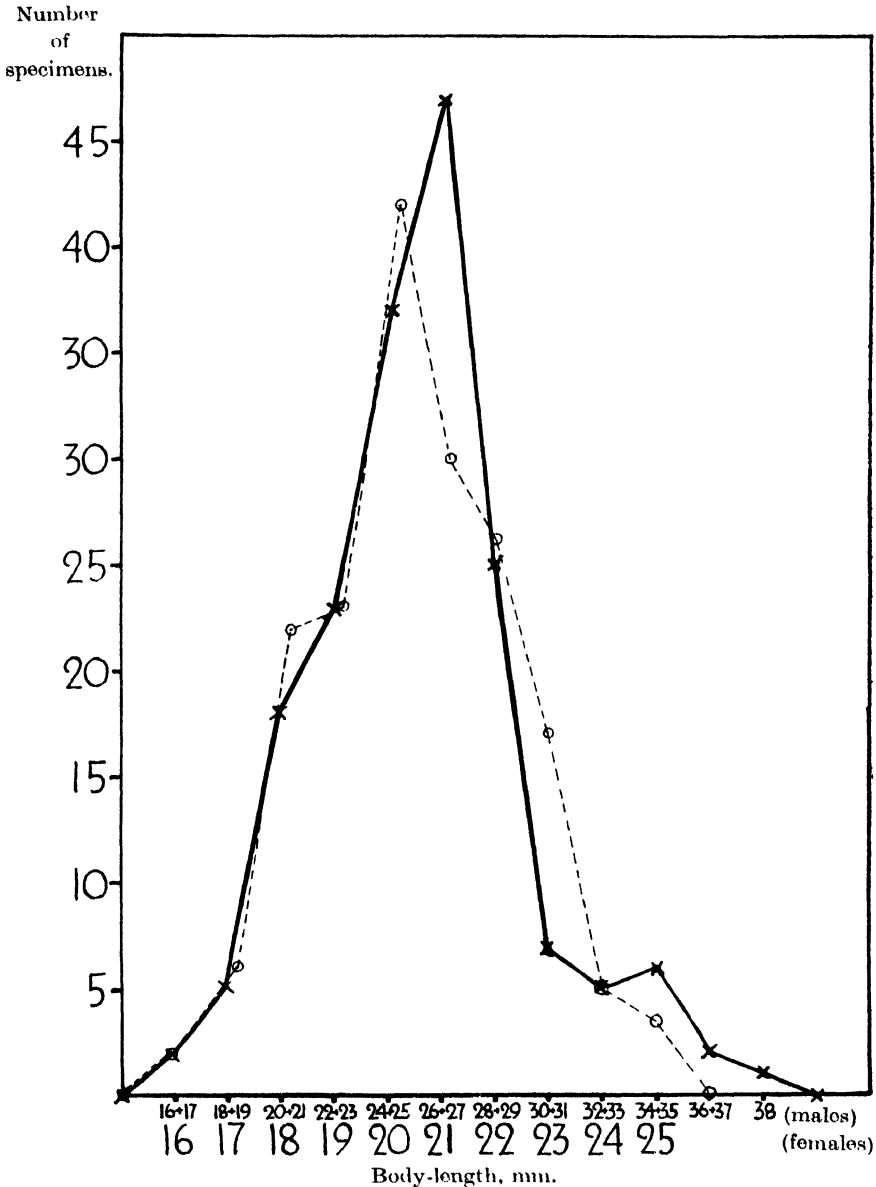
prionodonts of the same body-length. But this is presumably to be explained by the same degrees of variability existing as regards the relation between mandible-size and mandible-form (dentition) as exists between body-size and mandible-size.

The difficulty as to the transgression of body-size of the different forms comes simply from first assuming that the forms have a real biological existence and are not members in a continuous series, which naturally, however, shows normal variability. The overlapping like tiles of separate curves within the population is not a real phenomenon : it springs from the classification adopted. When the mandible-lengths of *every individual* are plotted against body-length in one graph, the result (not reproduced) is a regular figure bounded by two quite smooth lines, with no indication whatever of discontinuities at the transition from one form to another.

Dudich contrasts the morphologically characterized "forms" of *Cyclommatus* with the size-forms of other Lucanidae, assigning biological value to the former only. The analysis here adopted would tend to show that this view is not correct, that it is a mere accident whether the different-sized mandibles have different morphological characters or not, and that in both cases the whole mandible-series is continuous and of no systematic value.

We next come to the second difficulty—namely, the irregularity of the frequency-curve for male body-size as contrasted with the comparative regularity of that for female body-size. It is in the first place to be observed that the irregularity is quite probably in part due to the great range of the males' size. In the male there are 24 body-length classes of 1 mm. : in the female 10. When the data for the male are regrouped by 2 mm. classes, the multimodality largely disappears : though, on the other hand, the curve remains rather asymmetrical, bulging on the left, and prolonged further to the right with a slight but distinct subsidiary mode at 34.5 mm. (text-fig. 3). *Per contra*, when the female data are regrouped by 0.5 mm. classes, a rather distinct secondary mode appears at 18.5 mm. (which in the curve as grouped by 1 mm. classes causes a definite bulge), and another, more irregular, at about 22 mm. When the frequencies for male body-length (1 mm. classes) are separately plotted for each of the mandible-forms, a further interesting feature is revealed (text-fig. 4). Those for amphiodonts, telodonts, and mesamphiodonts are all themselves bimodal ; and, what is more, the low mode of the telodonts coincides with the low mode of the amphiodonts, the high telodont mode not only with the high amphiodont mode, but also with the single mesodont mode. If instead of plotting body-length frequencies, we plot those for "total" length (body-length+mandible-length) it is interesting to find that both the asymmetry and the distinctness of the multimodality of the curve are increased. The "total" length ranges from 20 to 74 mm. When grouping is by 2 mm. classes, the main mode is at 46 mm., with two sharp subsidiary modes at 32 and 38 mm., and another at 66 mm. When the data are grouped by 4 mm. classes, the multimodality persists, the two low modes coalescing into one, and the very high mode in the 60's still being noticeable.

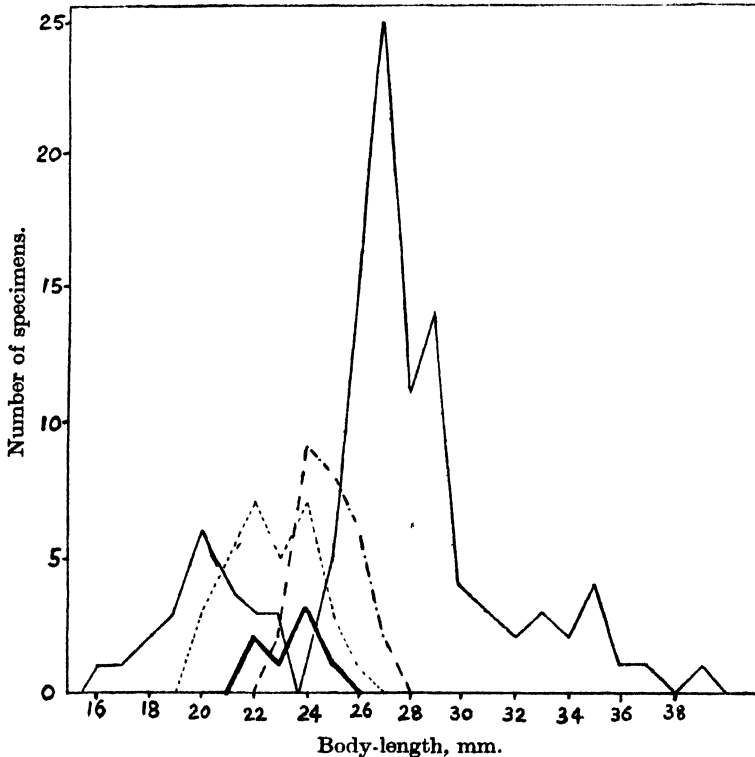
TEXT-FIG. 3.

*Cyclommatus tarandus.*

Frequency-curves for body-length. Solid line, 178 males, by 2 mm. classes; dotted line, 176 females, by 1 mm. classes. The male curve has a subsidiary mode to the right. The female curve shows no sign of this: and, as its horizontal scale is twice that for the males, shows much less variability.

The frequency-curve for the mandibles grouped by 1 mm. classes is given by Dudich (in his fig. 5). It is very irregular, with the main mode at 20 mm., several subsidiary modes between 8 and 14 mm., and a clear high mode at 28–29 mm. The multimodality persists markedly when the grouping is by 2 mm. classes (text-fig. 5). The shape of the total length curves and the mandible-curves are fairly similar; that of the body-length alone is much

TEXT-FIG. 4.

*Cyclommatus tarandus*, male.

Body-length frequencies plotted separately for the five growth-forms. A, thin solid line on left, prionodont; B, -----, amphiodont; C, thick solid line, telodont; D, - · - · - · -, mesodont; E, thin solid line on right, mesamphiodont.

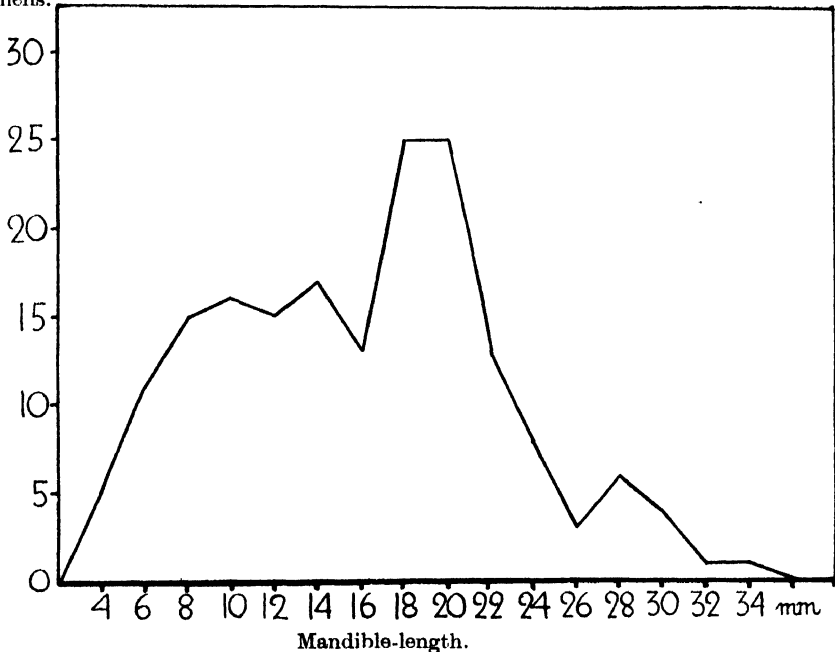
smoother. It would therefore appear as if we were presented with a situation not unlike that found in the earwig, and still more in *Xylotrupes*, in which the heterogonic appendage has a markedly bi- or multi-modal frequency, while the rest of the body has a distribution close, or at least closer, to a normal frequency-curve. As the multimodality affects such diverse organs as forceps, cephalic horn, and mandible, the reason must be not in the nature of the organ but in the heterogonic method of growth.

The frequency-curve for 115 mandibles of *Lucanus cervus* given by Bateson and Brindley (their fig. 6) is a good approximation to a unimodal normal frequency-curve. We shall later discuss possible reasons for this difference.

The tendency in *Cyclommatus* for the body-length curve itself to be multimodal is unusual. It is quite possible that as D'Arcy Thompson (1917, p. 106, note) and Przibram (1927) have suggested for the earwig that the cause is to be sought in a varying number of moults, each mode corresponding to a moult*.

Number of
specimens.

TEXT-FIG. 5.



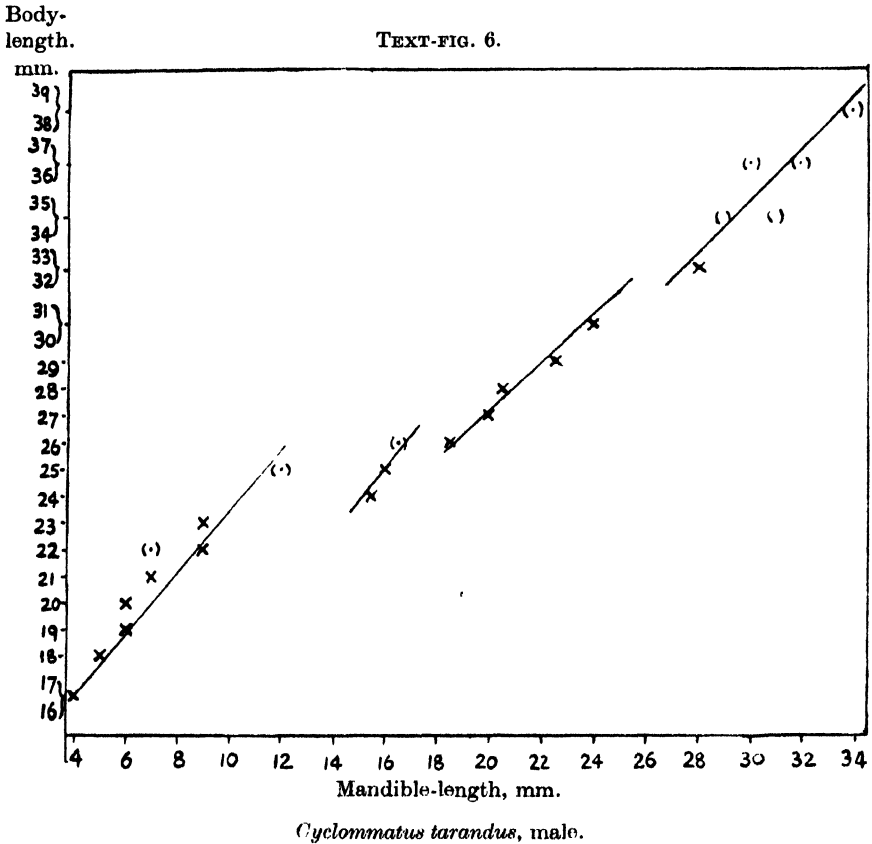
Cyclommatus tarandus, males.

Frequency-curve for mandible-length, by 2 mm. classes. The "4" class includes 4 mm. and 5 mm. mandibles, and so on.

In *Cyclommatus* then both the greater range of size of the male and its greater tendency to multimodality in the frequency-curve would be due to the variation in moult-number being greater in male than female larvæ. Whether this is so or not, however, the fact that several of the separate mandible-forms themselves exhibit bimodality in body and total length, and that their modes may coincide, indicates that it is not the different forms *per se* which are here of biological importance, but the *modal total sizes*.

* It is difficult, if this is so, to see why in the earwig the forceps are so distinctly bimodal, the body-length so beautifully unimodal: see later.

The fact that amphiodonts overlap telodonts both above and below in respect of body-length, and that both show bi-modality of body-length, indicates that the relation between body-size and mandible-size and that between mandible-size and mandible-dentition vary independently of each other, as would be expected. It does not interfere with the correctness of Dudich's interpretation of the sequence of the forms. He, clearly with reason, separates the two merely superficially similar forms, amphiodont and mesamphiodont; while



Modes of mandible-length frequency for each body-length class. x, main modes; (.), subsidiary or equal modes. (From Dudich's table, No. 4.)

Leuthner (1885) and Kolbe (1903) had lumped them together, and had also put telodont after mesodont. On the other hand, he speaks of *prionodonta* as "the most primitive" form, though he hesitates to draw the conclusion that the series is an evolutionary one. It *may* be an evolutionary one, but, if so, only as a secondary result of size-increase; and it is quite possible to argue that the "primitive" form was the medium-sized male mandible, from which the prionodont type is as much a special (size-) development as is mesamphiodont.

When Dudich speaks of the fallacy of trying to classify *Cyclommatus tarandus*

males into size-forms (his p. 75) he falls into the error of using body-length as his criterion instead of some measure of total size. The reason his amphiodont class includes forms with a greater body-length than his telodont class is simply because one form of body-length 26 mm. (the largest of the scarce telodont type being only 25 mm.) had an exceptionally small mandible of 11.8 mm., which, of course, being so small, was then of amphiodont type ' (see text-fig. 4).

I assume then that the mandible-forms of male *Cyclommatus* all really constitute a continuous function of mandible-size, and that this is fundamentally heterogonic. There is also an indication of the preponderance of certain body-sizes, and, more markedly, of certain "total" and mandible sizes.

On the other hand, it is not possible to find such clear evidence of multimodality as in *Xylotrupes* or still more *Forficula* when the frequency of the various lengths of the heterogonic organ is plotted separately for each body-length class (see Huxley, 1927 (c) (*Xylotrupes*), fig. 1; Huxley, 1927 (a), fig. 1). This is true whether the correlation is made between body-length or "total" length and the mandible-length.

All one can say is that the frequency-curves (not here reproduced) are mostly not at all regular, sometimes markedly skew (e. g., for body-lengths 26+27 mm.), or with reverse asymmetry (for body-length 20+21 mm.), or with a tendency to bimodality (e. g., for body-length 24+25 mm.).

It is clear that, though *Cyclommatus tarandus* is tending to a multimodality of heterogonic organ, the equilibrium-positions of the organ are not nearly so sharply defined as in Earwigs or even *Xylotrupes*.

On the other hand, the fact that equilibrium-positions exist may be shown in another way, by plotting the *modes* of the mandible at each body-length against the body-length (text-fig. 6). Subsidiary modes are also indicated where such exist. Instead of the modes falling on a single regular curve, they are clearly distributed on a number of discontinuous segments. At least 4, possibly 5 or 6, such partial curves may be distinguished. The mode thus tends to slip upwards rapidly ("discontinuously") several times as the body-length increases, while changing as a continuous function of body-length in between these points of discontinuity or rapid change.

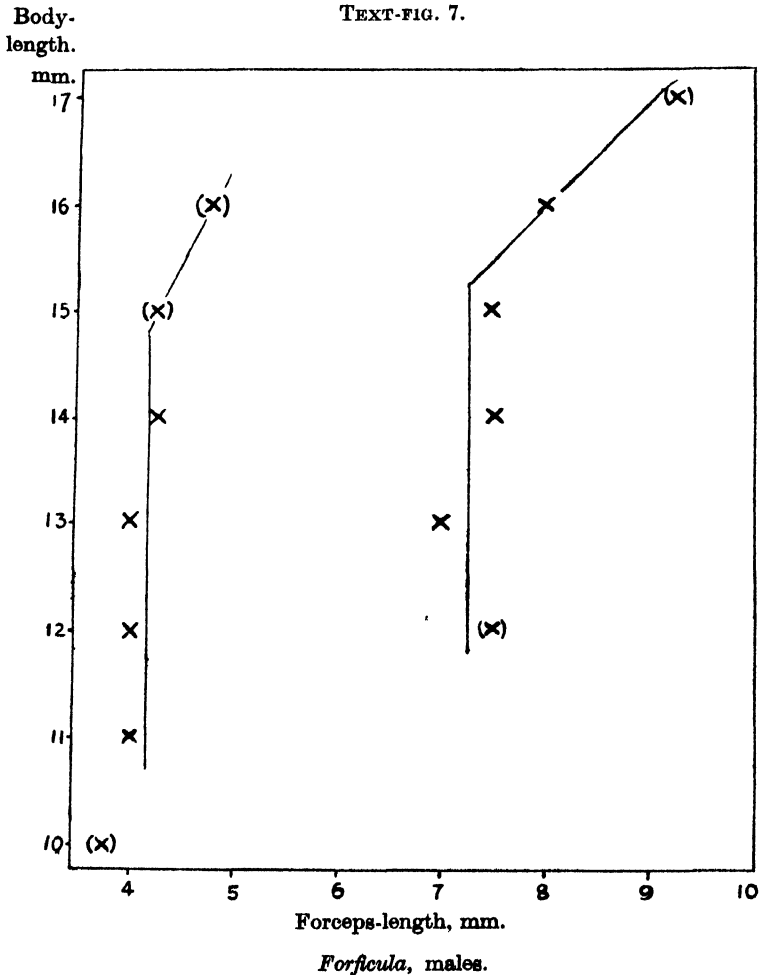
It is interesting to compare the curve thus obtained with similar curves of modes for *Forficula* and *Xylotrupes* (text-figs. 7 & 8). In *Forficula* two almost parallel vertical curves, overlapping for most of their extent, are obtained. In *Xylotrupes*, two main curves, hardly overlapping, but roughly parallel and inclined at a little over 45° to the horizontal, are seen, with an irregular number of subsidiary modes in the region of discontinuity. In *Cyclommatus* the discontinuities are not so great as in either of these cases.

In *L. cervus* no evidence of discontinuity is seen when the modes are thus plotted. This, however, may be due to the small total of specimens (48).

Further evidence of discontinuity may be found, though not so strikingly, when body-length frequencies are plotted for each size of heterogonic organ. This is best shown in *Xylotrupes*, in which there seems to be a main curve for

modal body-size from mandible-sizes 8 mm. to 22 mm., and two subsidiary curves, one at lowest sizes, one at highest, each slightly overlapping the main curve (graph not reproduced).

In *Forficula*, no definite evidence of this can be obtained. On the totals (my Table L, A-E) the mode of the body-size is 14.0 mm. for all forceps-sizes



Modes of the mandible-length frequency for each body-length class. x, main modes; (x), subsidiary modes or those based on small numbers. (From Huxley, 1927 a, fig. 1 B.)

from 4.5 to 7.0, and then is 14.5 to 15.0 up to forceps-size 9.0. At both lowest and highest forceps-sizes there is, however, a rapid change of modal body-size with forceps-size. This may be correlated with the existence of the two small subsidiary modal curves in *Xylotrupes*. The body of *Forficula*, however, is not

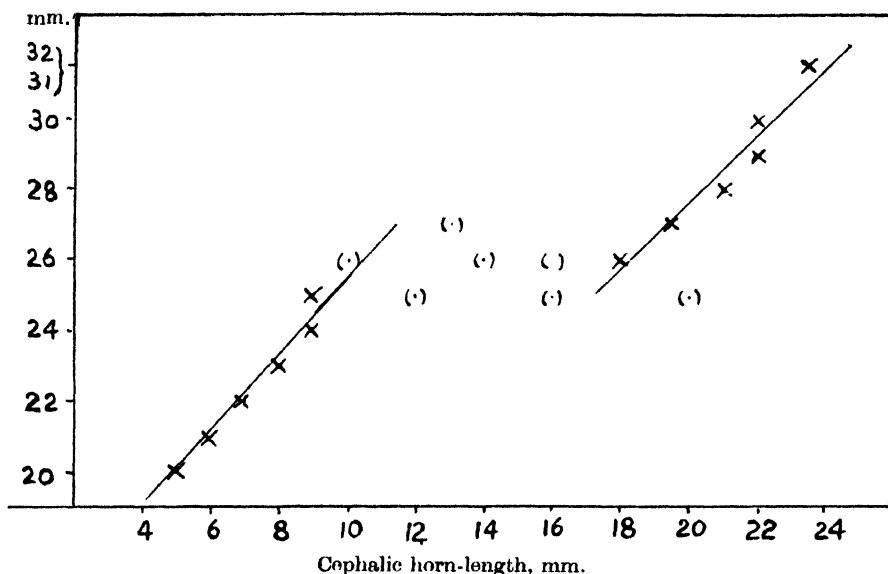
a very good object for accurate measurement. In *Cyclommatus* there is the same general tendency—a main central curve, with aberrations, possibly indicating discontinuities, at either end.

In *Cyclommatus*, a state of affairs rather similar to that in *Xylotrupes* is found. The curves are not very regular, but there are indications of three or four curves for modal body-size, when body-size frequency is plotted against mean mandible-size.

Let us now consider the possible reasons for bi- or multi-modality. In *Inachus dorsettensis*, Shaw (1928) found a bi-modal frequency-curve for female abdomen breadth. What happens during the growth of the abdomen in this form seems

Elytron-length,

TEXT-FIG. 8.



Xylotrupes gideon, males.

Modes of cephalic horn-length frequency for each class by elytron-length. ⊙, main modes ; (·), subsidiary modes. (From Huxley, 1927 c, fig. 1, utilizing only Bateson and Brindley's specimens.)

to be as follows:—(a) During early life, the female shows a low but definite degree of heterogonic growth, which removes it gradually from the male type (relative abdomen-breadth about 20 per cent. of carapace-length) to an adolescent or "low" female type whose mean relative breadth eventually reaches just over 40 per cent. (b) Then follows a moult at which the mean relative breadth suddenly jumps to over 65 per cent., and after this stays approximately constant. No crabs at all were found with abdomens between 45 per cent. and nearly 65 per cent. in relative breadth. These facts can only be explained if (c) the changes responsible for the rapid increases of abdomen-size all take place

during a single instar, and are therefore invisible until the next moult: and (d) are initiated at a more or less constant phase of the instar, presumably soon after the previous moult.

Consideration of the absolute size of the adolescent and mature type crabs indicated that the moult at which the critical changes were initiated was probably not fixed, but could be either the n th or the $n+1$ st, since abdomen-bimodality was found from 13 to 17 mm. carapace-length, a size-difference corresponding on Brooks's law to one moult-stage.

A similar but less marked bi-modality without discontinuity appears in the chelar propus of males. Here again the explanation would appear to be similar: that during one instar only, there is a marked growth-promoting influence acting on the chela, which, of course, can only show its results after the next moult.

These facts are of importance, since they show that the discontinuous growth produced by moulting can introduce bi-modality or even complete discontinuity into the frequency-curve for the size of an organ, even in animals without metamorphosis and with no fixed adult size or form.

Let us now apply these results to animals with metamorphosis. The most clear in these is that of the earwig. In the female, the larval forceps are converted with very little alteration in size into the imaginal form; thus here there is no opportunity for bi-modality to occur. In the male, however, some preparatory growth-influencing process must have occurred during the later part of larval life, since, on moulting into the imago, the forceps are found to be markedly larger.

Thus, even in a population entirely composed of "low" forms, there is already a bi-modality comparable to that seen in *Inachus*—a bi-modality of successive stages, one being the larval, the other the imaginal: this, however, is not bi-modality in the usual sense—viz., bi-modality of imagines.

The problem is further complicated by the existence of bi-modality among the imaginal forceps themselves*.

Przibram, as we have seen, suggests that this is due to there being an extra moult intercalated in the life-history of the "high" types. This explanation

* I am aware that Kuhl (1928) has attempted to deny the bi-modality of the male forceps in *Forficula* on the grounds that unconscious selection of large specimens in making the collections would cause a second "high" mode. This appears to me out of the question, as it does not explain why other parts of the body do not show bimodal curves, nor why the female are consistently uni-modal. The explanation appears to me to be that in his collection he has been dealing with populations which happened to be mainly of low type. Djakonov (1925) and Bateson and Brindley (*l.c.*) both found that 7.0-7.5 mm. was the modal length for the "high" forceps; but Kuhl's Heligoland specimens had less than 1 per cent. of forceps over 5.5 mm., his Frankfurt specimens less than 1 per cent. over 6.5 mm. Even these, however, showed highly asymmetrical frequency-curves, *i.e.*, they would have been bi-modal if there had been more specimens of high type; and in his Holstein set, where the forceps-range just reaches 8 mm., there is a distinct second mode. I regard the bi-modality of Earwig forceps as a proved fact.

in this simple form, however, suffers from two defects. It does not explain why the body-size is not bi-modal also. And he appears to think that "high" and "low" forceps types are in some way morphologically distinct, whereas, in point of fact, there is a complete transition between them.

I would suggest that the explanation of an extra moult is correct, but needs further hypotheses to bring about the observed result.

Let us suppose (1) that the processes influencing the rapid growth of the male forceps are always initiated, as those for *Inachus* female abdomen, at a fixed

TEXT-FIG. 9.

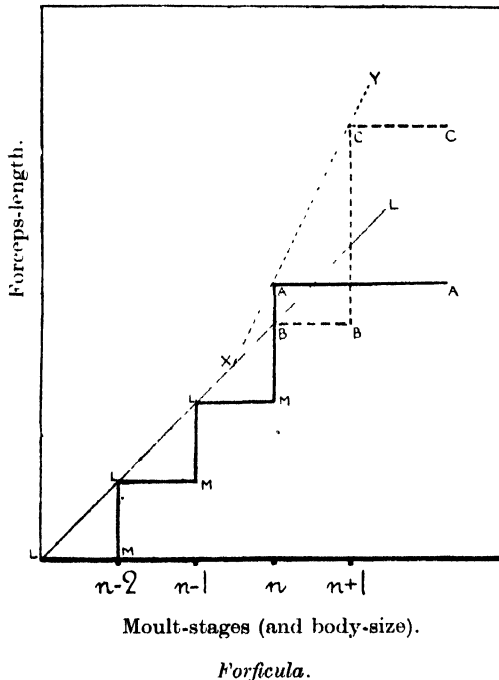


Diagram of suggested explanation of forceps-bimodality in males. LM, LM . . . , larval forceps of proportionate (isogenic) growth of forceps-size with body-size; X, point at which heterogonic growth (XY) of male forceps is initiated. If the change to the imago occurs at the n th moult the level of forceps-size is at A-A ("low" forceps): if at the $n+1$ st moult the forceps, after continuing of larval type for one more instar (B-B), reaches the size-level C-C ("high" forceps).

time soon after a moult, and that this moult is late in the animal's larval life; (2) that the conversion into adult male-type forceps can only occur at the assumption of the imaginal state: (3) that the assumption of the imaginal state can occur either at the next or the next-but-one moult after the growth-influencing processes have been initiated. Then we shall have the result shown in text-fig. 9. The growth-influences either act for a fraction of one instar, or for one whole instar plus this same fraction. They are brought

to an end by the assumption of the imaginal form, with consequent bi-modality. The number of previous moults being considerable, the normal variations in growth-rate will obscure any tendency to bi-modality in body-size.

There remains to be accounted for the singular fact that if we take the "high" or "low" forceps *separately*, the percentage size of forceps *decreases* within both of the groups with increasing body-size. This may perhaps be accounted for owing to time-relations. If the moult after which initiation of the growth-influencing processes begins may occur over a considerable range of size, then we may imagine that the only effect will be for their velocity to be somewhat higher when absolute body-size is greater. But if they can only operate during the *time* provided by the remainder of the instar: and if the consequent increase in forceps-size be not so great as the difference in body-size at the beginning of the growth-influencing process, the larger specimens, provided that the subsequent number of instars before reaching the imaginal state remains the same, will have relatively smaller though absolutely larger forceps. The biggest of those with less than one subsequent instar will have relatively smaller forceps than the smallest; but all those with less than *two* subsequent instars will, of course, have much bigger forceps, relatively and absolutely, than those with less than one.

If the increase in velocity of the growth-influencing process due to increase of absolute size were greater, this effect would not occur, but within both high and low groups, taken separately, relative size of organ would increase with absolute body-size, though, of course, not nearly so rapidly as when means for both groups together are taken. This apparently is what happens in *Xylotrupes*.

Further, in *Xylotrupes*, and still more in *Cyclommatus*, the phenomenon is less regular. Instead of clear-cut bi-modality, we have rather confused multi-modality. It is noteworthy that, in both cases, the body-size range is very large; in *Xylotrupes* the highest body-size is nearly 2.1 times the smallest, while in *Cyclommatus* the figure is nearly 2.5. This would imply that the variation in possible moult-number is greater in these forms. If, in addition, there were more variation in the stage of onset of the change influencing horn- (or mandible-) growth, we should have a provisional explanation for the greater irregularity of the resulting frequency-curves.

The difference between the Lucanids (and other forms) which are pœcilandrous (with several male types: di- or poly-morphic) and those which are not pœcilandrous (with only one true male type: monomorphic) would then be due to the fact that the males of monomorphic forms all normally had the same number of moults, whereas the moult-number was normally variable in the pœcilandrous types.

Przibram has shown that primitively Arthropods double in bulk at each moult, which means that they increase their linear dimensions in the ratio of 1.0 to 1.26, or roughly from 4 to 5 (Brooks's law). In some higher insects, however, it has been shown that the bulk is roughly quadrupled at each moult—

a fact apparently made possible by the soft larval integument. This would mean an increase from 1.0 to 1.59, or roughly from 5 to 8, in linear dimensions. The following figures are of interest in this connection. In Bateson and Brindley's 48 *Lucanus cervus* the ratio of largest to smallest elytron-length is 1.31 (excluding one extremely small specimen: 1.6 if this be included). In the 18 *L. lunifer*, the ratio is 1.36. In *Cyclommatus tarandus*, on the other hand, the corresponding ratio for body-lengths is 2.47.

If for body-length we substitute "total" length ratios, the figures become: for *L. cervus* 1.41 or 1.77 according as we exclude or include the very small specimen; for *L. lunifer* 1.54; and for *C. tarandus* 3.75. It is thus clear that the supposition of a greater variability of moult-number in *C. tarandus* is supported by the facts. One might also hazard the supposition that the aberrant small *L. cervus* has had one moult fewer than its congeners; but this is, of course, pure speculation.

Bateson and Brindley pointed out that whereas the "low" males of *Xylotrupes* and *Forficula* approximate in regard to their secondary sexual appendages to the females, the lowest of their *Lucanus cervus* had mandibles much larger than the females. The same is the case for *Cyclommatus*, judging from Dudich's figures—i. e., the greater range of *Cyclommatus* over *Lucanus* is due to extension at the high end of the scale. The differences noted by Bateson and Brindley must depend upon the time-relations of the processes initiating heterogony in relation to moult.

If Przibram's view is correct, then we shall get poly- (di-) morphism of imaginal form under the following conditions: (1) when a heterogonic organ exists in the imago only; (2) when the number of moults is variable; (3) when the rudiment of the heterogonic organ begins its heterogonic growth at a definite time after a late moult.

The more definite the relation is between a particular moult and the moment of onset of heterogonic growth, and the later this particular moment is in the life-history, the more sharp will be the polymorphism.

(5) GENERAL CONCLUSIONS.

The chief points which seem to emerge are the following. In the first place, the growth of the mandibles of male Lucanidæ shows a close approximation to the simple heterogony formula. The approximation is excellent while the animals are small, and the mandibles therefore relatively small. In the higher-size classes, however, there is an unmistakable tendency for the actual values of mandible-size to fall short of those theoretically expected, and for this tendency to become progressively exaggerated. The reason for this apparently lies in the fact of total metamorphosis.

In all Lucanidæ, the increase in mandible-size brings with it modifications of mandible-form. These may be mainly confined to the "teeth" of the mandible, or the mandible's whole shape and curvature may be altered. The various

taxonomic forms erected on the basis of such alterations in the mandible have no systematic significance; they are merely effects of the existence of the developmental mechanism for heterogonic mandible-growth, and accordingly the "forms" represented in any one locality or season will merely reflect the absolute size of the beetles, and therefore primarily the favourable or unfavourable conditions of the environment.

There will exist, of course, variations. These may be of various origins. (a) In the first place, slight variations, well within the normal range of variability of a wild species, may be expected in the values of b and k . Variations in b may be due to variations in the time of first appearance (or determination) of the heterogonic growth of its rudiment. Variations in k will be due to variations in the growth-rate either of the heterogonic organ or of the body or both. The results, however, of variations either in b or in k will be the same. Higher values than normal will produce mandibles larger than normal at a given body-size, and *vice versa*.

If, as has been assumed, absolute size of mandible is the chief factor responsible for alteration in the form of the mandible, then the variations in b and k above referred to will bring it about that at a given body-size some animals may have mandibles sufficiently larger than the normal for that body-size to fall into a different form-class.

This will inevitably cause an overlap in body-size of two adjacent form-classes, even in animals from the same locality. Larger variations in b and k might be expected from different geographical localities. In this case the overlap would be much greater, and the picture given by a mixed population from two or more localities might be hopelessly confused (see for similar effects in *Xylotrupes*, Huxley, 1927 c).

(b) Variations may also be expected in the way in which morphological changes in the mandible are brought about by increases in size—*e. g.*, the passage from one form to another may occur at a smaller or a larger mandible-size than normal. This will tend to accentuate the overlap caused by variations in b and k .

(c) There may also exist variations in the character of the morphological change brought about by a given size-increase. To take an imaginary example. if a new tooth appears after a given mandible-size, this tooth may in some cases be long, straight, and pointed, in others be short, curved, and blunt. Those variations would be expected to be due to gene-mutations affecting form-detail, and to be independent of the heterogony-mechanism.

The systematist in search of subspecies and local races should therefore begin by determining the constants b and k for a number of local populations. Marked local differences in these values will be true systematic race-characteristics. In addition, he should examine these local populations for evidences of a passage from one growth-type to another *at different absolute mandible-sizes*. For instance, in the population measured by Dudich, the length of prionodont mandibles ranges from about 4 mm. to 10 mm., that of amphiodont from below 8 to over 12 mm., that of telodont from 11 to about 15 mm.

Now suppose that in another population the prionodonts had ranged up to 12, the amphiodonts up to 14.5, and the telodonts up to 18 mm. This would have clearly indicated a different quantitative relationship of morphological change to mandible-size, and could be legitimately taken as a racial character.

If, finally, when allowance had been made for the above types of variation, it was found that in mandibles of the same growth-type there were constant differences of form-detail, these would also be valid racial characteristics. But the growth-types *in themselves* can never be taken as systematic divisions. The only case where they might have a systematic value (and that an indirect one) would be if in one locality one or more of the large growth-types were absent, in another one or more of the small growth-types. This would naturally be correlated with variation in absolute body-size. The systematist in such a case would first have to determine whether the variation was genetically or environmentally determined. If genetically, he would then be in the presence of a racial difference in absolute body-size, whose indirect effect was visible in the range of growth-forms produced.

(6) SUMMARY.

(1) Linear measurements of length of mandibles and body (or elytron) made by Brindley, myself, and Dudich, respectively, in the males of three species of Lucanidae, have been analysed. It is shown that the simple heterogony formula $y = bx^k$, where y = mandible-length, x = "total" length (mandible-length + body-length), and b and k are constants, provides the basis for an expansion of mandible-growth. The values of k are, for *L. cervus* about 2.3, for *L. lunifer* about 1.55, for *Cyclommatus tarandus* 1.97.

(2) The approximation of actual to expected figures is close for the smaller individuals of each species. In all cases, the curves bend over in the higher part of their range, the actual mandible-size falling progressively more and more below expectation. This, it is suggested, may be accounted for owing to the limited amount of food-material in the pupa being exhausted before very large mandibles can be formed.

(3) In the holometabolous insects, such as Lucanidae, it is assumed that the heterogonic relation between mandible and rest of body is produced in one of two ways—either by the formation of a substance responsible for heterogonic growth of the mandible-rudiment, continuously throughout larval growth at a heterogonic rate : or by the sudden appearance of heterogonic growth in the rudiments of the imaginal mandibles at a definite stage during the pupal stage. Experiments on larval nutrition are needed to decide this point.

(4) The chief way of handling data for heterogonic organs in holometabolous insects are discussed.

(5) As result of these facts it is concluded that the "forms" of male Lucanids distinguished by coleopterists are purely growth-forms and have no systematic significance.

(6) A tendency for multi-modality is evident in the frequency-curve for the mandibles of male *Cyclommatus tarandus* ; this appears to be correlated with the greater range of body-size in this species and consequent presumed greater variability of moult-number, as compared with the other Lucanids studied.

(7) D'Arcy Thompson and Przibram's theory, which sees the cause of bi- (multi-) modality of heterogonic organs in a variation in moult-number during larval life is extended to make it fit the facts, and is further generalized.

[POSTSCRIPT.—Teissier (1931), whose work did not appear until after this analysis was complete, has also dealt with the heterogony of the mandibles of *L. cervus*. He has, however, only dealt with the weight-measurements of the desiccated parts. His results, based on 40 specimens, give a good approximation to the simple heterogony formula, the value of k for mandible-weight against elytron-weight being 2.0.

The shape of his curve is of considerable interest. On logarithmic coordinates it is a close approximation to a straight line, without any inflection at high values. This may be due to his plot not having enough specimens (this cannot be discovered from his text-fig. 20, since only weights are given ; but in text-fig. 21, where he is comparing linear measurements, his elytron-lengths vary from about 16 to about 28, whereas Brindley's range from 25 to 40). Or it is possible that the line of reasoning which I have adopted in Section 2 of this paper is incorrect, and that at large body-sizes the shape of the mandible becomes more curved, so that its length measured in a straight line would fall short of its true length, and weight would thus give a better picture of its relative growth than length. The objection to this suggestion is that in my curves the divergence from the straight line is only shown at high sizes, and is not progressive from the first, as it should be if the mandible gradually changed its shape. For instance, Dudich's figures, although they do show that the inner margins of the mandibles (the dimension he measured) in the smallest males *Cyclommatus tarandus* are straight, in the largest males curved, also show that a slight curvature is to be seen in the amphiodont, which increases progressively, being quite marked in the mesodont ; whereas the double logarithmic plot shows no deviation from a straight line until after the population is entirely mesamphiodont. In *L. cervus*, again, the increase of curvature with size appears to be slight, and not to be markedly accentuated in the largest forms.]

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Physiological Adaptation. By C. F. A. PANTIN, M.A. The Zoological Laboratory, Cambridge. (Communicated by Dr. G. P. BIDDER.)

[Read 14th May, 1931.]

ONE of the first duties in any science is the description of the objects with which that science deals. In Biology this demands an exact account of the living organism in relation to its environment. But, whereas we can speak of the morphological characters of an organism with considerable precision, the physiological characters which describe their functional significance and the adaptation of organism to environment remain ill-defined. The term "physiological character" covers many entirely different things, and it is our object to consider their nature and the ways in which they bring about physiological adaptation to the environment.

In the first place, it is necessary to define the term "adaptation." Few things seem more evident than its existence, but its exact definition is not easy. Perhaps the definition given by Allen (1929) in his Hooker lecture is best: "By an adaptation we mean nothing more than a character of an organism which has enabled a species to survive itself as such, or to survive until it is transformed into another species. It is survival that gives the measure of adaptation." This definition is simple and precise. At least in theory, it allows the quantitative determination of adaptation by direct experiment. It omits implications concerning the mode of origin of adaptations and of their apparent "purposiveness." A character is adaptive as long as it increases the chance of survival, even when it does so under unusual circumstances which the organism could never have been prepared to meet.

But we do not usually employ Allen's definition in practice. When we state that a particular character is an adaptation, we usually base our judgment on certain qualitative impressions. These are, first, an apparent correlation between the occurrence of a particular character and a particular environmental feature, and, secondly, our perception of some functional relation between them. Thus the occurrence of hæmoglobin in animals is definitely correlated with environments deficient in oxygen. We perceive also a functional relation based on the ability of hæmoglobin to combine with oxygen. We therefore argue that the occurrence of hæmoglobin is an adaptation to an environment poor in oxygen. Of two species of *Cucumaria*, *C. elongata* lives in mud which may well be deficient in oxygen and its coelomic fluid contains abundant hæmoglobin corpuscles. On the other hand, *C. saxicola*, which lives among rocks, possesses no hæmoglobin. The inference that the hæmoglobin in *C. elongata* is an adaptation to its environment seems natural.

Such judgments may, in fact, be attempts to make a qualitative estimate of the survival value of the character on a basis such as Allen's definition. But instead of performing direct experiments to determine survival value, we attempt to infer their answer from what we know of the properties of the environment and of the character concerned. In this there is great danger. Our knowledge of the environment of most organisms is very incomplete, and our ignorance is too often filled in by precarious assumptions based on the analogy of our own special environment. We cannot define "adaptation" to conditions which we cannot specify, and our attempted functional interpretation may be wrong unless verified by experiment.

Numerous correlations are found without apparent functional explanation. Many animals have free in their gut substances which yield hæmochromogens. Such are the helicorubin in the crop of *Helix* and the similar substances present in the digestive fluids of many Crustacea, of the worm *Aphrodite*, and other animals. If an ingenious functional significance were suggested for this, we might be tempted to consider it an adaptation. Because, in this case, no satisfactory interpretation is forthcoming, we can without prejudice perceive how much the truth of any such interpretation would require experimental verification.

In many cases physiological adaptation seems clear. Krogh and Leitch (1919) showed that the eel and pike, which can live in water somewhat deficient in oxygen, possess hæmoglobins with a much higher avidity for oxygen than that of the trout, which only survives in well-aerated water. But to dismiss such cases as adaptations without a functional study of animal and environment is to cloak ignorance. *Planorbis* and *Arenicola* both live under conditions of oxygen deficiency. Both possess hæmoglobin with a high affinity for oxygen. But its function is different in the two cases. Leitch (1916) showed that in *Planorbis* the hæmoglobin acts primarily as a carrier of oxygen from the surface of the animal to the tissues, which comes into action when the external oxygen pressure is so low that simple diffusion of oxygen no longer supplies the needs of the animal. On the other hand, Barcroft and Barcroft (1924) found in *Arenicola* that the function of the hæmoglobin is to provide a store upon which the worm can draw during the period it remains sealed in its burrow at low tide.

Like *Arenicola*, the Sabellid worms possess a respiratory pigment, in this case chlorocruorin. These worms are tubicolous, and one might be tempted to ascribe to the pigment an adaptational significance similar to the hæmoglobin of *Arenicola*. But Fox (1926) has shown that the affinity of the chlorocruorins for oxygen is so low that they are not even fully saturated when in equilibrium with air. We can only say we do not know their functional significance. Though physiological adaptation is a reality, the very facility with which hypotheses can be formed when knowledge of both environment and function is uncertain shows how necessary it is that experimental verification should immediately follow. Without verification the hypotheses purport to give knowledge we do not possess.

So long as this is continually borne in mind the search for adaptational significance of physiological characters is very productive. Recent work on the effect of temperature on the enzymes of various invertebrates illustrates this. Experiments of a few hours' duration with the enzymes of the mammalian gut show that the "optimum" temperature at which the greatest amount of substrate is digested coincides with the normal temperature of the body. But in various marine invertebrates, experiments of 2-3 hours' duration showed optimum enzyme action at temperatures of from 40° to 60° C. These are far above the death-point of the animals (20°-30° C.).

The idea that, despite appearances, the properties of these digestive enzymes might, nevertheless, be closely related to the conditions of existence of the animals led Berrill (1929) to reconsider the problem. He drew attention to the well-known fact that the "optimum" temperature of an enzyme depends on the duration of the experiment: the greater the duration the greater is the destruction of enzyme at high temperatures, so that the longer the experiment lasts the lower is the apparent optimum temperature. For the amylase of the Tunicate, *Tethyum*, the optimum conversion of starch after one hour occurred at 45° C. But after 57 hours the optimum temperature was as low as 13° C. Now at a temperature of 10° C., which is near that of the normal environment, the food required 50-55 hours to pass through the gut. It therefore follows that the enzyme is utilised as economically as possible under natural conditions. Similar conditions have been shown to obtain in *Sabella* (Nicol, 1930) and in *Pecten* (Graham, 1931).

But, despite the interest of these observations, the problem is still far from concluded. Provided the amount of digestion effected by the enzyme at ordinary temperatures be unaltered, no disadvantage would seem to exist if, in addition, it were able to withstand abnormally high temperatures without rapid destruction. We know, at present, no reason why an enzyme should not possess this property and yet retain a digestive efficiency at lower temperatures equal to that of the unstable enzymes actually found in these animals. Such an enzyme would be even more efficient at a higher temperature than at that of the normal environment: the "optimum" might be above the death-point. It is true that this property would never be of use to the animal, but, since the efficiency at ordinary temperatures is supposedly unaltered, this would seem of no disadvantage to the animal. Nevertheless, this condition does not seem to occur.

What the investigations have shown is that certain physiological characters are directly related to environmental conditions. But the problem of their adaptive value—that is, how far they would affect survival—is not concluded. It is important to notice that the next stage of this problem must involve purely laboratory experiments on the physical properties of enzymes. In the study of function under natural conditions, the biologist may not neglect the physical nature of the systems concerned, even though this involves experiments under artificial conditions quite foreign to those found in Nature.

Having surveyed some of the grounds on which physiological adaptation may be inferred, we may consider the nature of the physiological characters by which it is specified. The living organism comprises material structures of different orders of complexity, varying from tissues and cells to particular kinds of molecules which compose them. A variety of active processes takes place in these structures, and their existence depends on them. Conversely, the structures themselves have been brought into existence by such processes. By these processes certain states are actively maintained by the organism. These structures, processes, and states endow the organism with certain properties, so that when subjected to a particular experimental treatment it reacts in certain definite ways.

Morphological characters simply refer to material structures. But among physiological characters entirely different kinds of things are apt to be taken according to what aspect of the living organism happens to strike the observer. For convenience they may be considered in four groups: physiological "structures," such as molecules of a respiratory pigment; "processes," particularly those of metabolism; "states" actively maintained by the organism, such as the ionic composition of the blood; "properties," such as limits of temperature or pH within which the organism can survive. Of these, the structures and the properties of the whole organism are most usually seized upon, and attention will be directed chiefly towards them.

Like morphological structures, physiological structures are material bodies. The fact that these may be molecules provides no fundamental distinction between them except order of complexity. Indeed, comparative anatomy cannot logically be limited to structures above an arbitrary size. Just as gross anatomy extends to the cellular nature of tissues, and the structure of the cell to its microscopically visible constituents, so the study of form must extend further to the ultimate molecular morphology of cell-structures. Atoms and electrons are the common material of all living organisms. It is in the structure of the molecule that specific differentiation first becomes apparent. For this reason the description of molecular structure occupies a position of peculiar importance in the systematic description of organisms. We may not limit such description to macroscopic structures simply on the ground that its extension involves the biologist in methods with which he is unfamiliar. Nuttall's (1904) classical work on blood-immunity indicated that in different animals complex molecules may undergo differentiation that is quite comparable to specific morphological differentiation, and follows phylogenetic relationship in the same way.

We are apt to consider morphological characters as infinitely plastic in their capacity for differentiation. Yet this cannot be true of molecular structures, because they are composed of units. Despite this limitation, immense variety is possible. Proteins are the most complex constituents of protoplasm. The molecule is composed of amino-acids, of which there are known some twenty-one different kinds. Their molecular weight is probably always

1, 2, 3, or $6 \times 34,500$ (Svedberg, 1930). Since the average molecular weight of an amino-acid is 90 to 100, it follows that each protein molecule is an aggregate of units each containing some 350 amino-acids. The number of ways in which twenty-one different kinds of object can be arranged in series to form units of 350 is about 10^{450} . These in turn can be arranged to form aggregates of 6, 3, 2, and 1 units in about 10^{2700} ways. This number is, therefore, the general order of the different proteins which might be possible to our present knowledge. It is inconceivably great. (According to Eddington there are only 10^{79} electrons in the whole Universe!) Almost infinite gradations of protein structure are rendered possible. Nevertheless, the whole nature of the molecule is limited, because it is composed of units. Though organisms have evolved proteins with specific gradations of structure, evolutionary modification must have occurred by abrupt steps of one or more amino-acids.

The limitations imposed by molecular structure are very clear in substances such as the respiratory pigments, which subserve a unique function. These are remarkably limited in kind. Only four classes are definitely known which are able to combine reversibly with oxygen. These are: the hæmoglobins, the chlorocruorins, the hæmerythrins, and the hæmocyanins. The first three contain iron and the last copper. All the members of one class are closely related compounds of characteristic structure, and are quite distinct from the other classes.

In considering these pigments some striking features appear. When an animal develops a respiratory pigment it seems strictly limited to one of four classes of molecule. Further, the same pigment is independently evolved in entirely distinct groups of animals. We have here a character of great adaptational significance, which has evolved repeatedly and which could not possibly be developed gradually. Only in the complete molecule do the peculiarly valuable oxygen-carrying powers emerge. However perfectly the presence of hæmoglobin may appear to adapt the animal to its environment, it could only have arisen by the sudden appearance of the complete molecule.

The analysis of these systems is of interest. The molecule of hæmoglobin is a combination of a particular iron-porphyrin compound with protein. The protein varies in different organisms and causes small variations in the physical properties of the molecule. The iron-porphyrin compound has a unique structure, identical in all hæmoglobins. This same compound also appears in all kinds of protoplasm in free hæmatins, hæmochromogens, and the respiratory substance cytochrome. It seems, therefore, that the occurrence of hæmoglobin is determined by the fact that only limited materials are available in protoplasm for the construction of a respiratory pigment. Since the iron-porphyrin compounds only require a particular combination with certain proteins to yield hæmoglobin, this substance appears repeatedly.

The limitations of the materials available in protoplasm arise from the properties of matter. In the periodic table very few elements are available

for the construction of protoplasm, and each has highly special properties. It is the special properties of iron that render hæmoglobin possible; no other element can adequately take its place.

Our consideration of physiological structure forcibly makes us consider that protoplasmic materials comprise a limited number of standard parts of limited properties. Only certain molecules can be constructed from these to meet any special function. No infinitely graded adaptation is possible in these units, so that special structures must appear fully developed or not at all. Owing to the numerous units employed, an immense number of gradations in properties may be observed in related complex molecules such as the proteins. But these molecules can only be made of certain kinds of units and only modified by whole units at a time. We realise that the organism can never be infinitely plastic. All its structures are makeshifts which meet environmental requirements within the limits of the standard parts available for their construction.

It seems that adaptation of these structures can only be evolved by the natural selection of abrupt variations—a condition precisely satisfied by Mendelian mutation. Provided the properties of the structure depend equally on a large number of units, slight variation in many directions is possible. But if the nature of one particular unit is all-important in determining the properties of the whole structure, successful variation becomes possible only along certain lines, as in the repeated evolution of hæmoglobin. It is noteworthy that even in complex morphological structures evidence for parallel evolution and for orthogenetic trends necessarily rests upon the results of one particular process—in this case the deposition of calcium compounds.

Within the limits of this essay it is not possible to discuss the adaptation of physiological processes and of the states they maintain. Their evolution and adaptive significance is of a different nature from that of molecular or gross morphological structure. Indeed, it is the latter alone that have undergone evolution and adaptation in the ordinary sense. For the processes and states only exist at any moment as a consequence of structure. Thus if we say that the ionic composition of the blood of an animal is adapted to the maintenance of the tissue-cells, it is, in fact, the surface membranes and excretory organs that have actually undergone evolutionary adaptation. Consequently adaptive significance of blood composition cannot be discussed till we have adequate knowledge of the structures which maintain it (Pantin, 1931).

Adaptation seems peculiarly evident in the physiological properties of the animal as a whole. These properties are inevitably noticed in any systematic description of the organism in its environment. Their interpretation is necessarily the most complicated, because they involve every character of the organism. An example of such properties is provided by the temperature range of survival of an organism. This range is closely related to the normal environmental temperature. Mayer (1914) showed in *Aurelia* that the limits of survival in the same species of organism may differ greatly according to the normal environmental temperature where the organisms are found.

The adaptation of organisms to temperature is peculiar in that the death-point seems always but little above the highest temperature to which the organism is normally subject. But experiments similar to those of Mayer, and of Dallinger (1887), show that over a long period a species can, in fact, become gradually adapted to withstand temperatures far above the death-point when taken from a cold environment, so that the normal closeness of the death-point to the environmental temperature must be actively brought about by the organism. It is not easy to see, from the point of view of survival, wherein failure to withstand abnormally high temperatures can be the result of adaptation. Provided survival is satisfactory at normal temperatures, there seems no disadvantage in ability to withstand much higher temperatures, even though they be never encountered. Animals do not seem to possess this ability. A search for the adaptational significance of temperature limits would be of the greatest interest. Perhaps the attention that has been paid to the evaluation of temperature-coefficients in organisms has obscured the very great importance of studying the factors which determine the temperature-limits.

In all such cases what we require is more accurate description of the organism and its environment. Only in the field can the conditions of existence of the animal be truly determined. But to determine the adaptational significance of its characters to these conditions, their physical nature must be analysed in the laboratory, even though the experiments may seem far removed from the actual conditions of the animal.

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[Synonyms are printed in *italics*. A star * denotes the first publication of a name; a dagger † denotes a fossil. The absence of an authority is due to omission by the respective authors.]

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